

SYSTEMATICS OF HOLOGRAPHIS (ACANTHACEAE)

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MEXICAN ACANTHACEAE have received little taxonomic attention since Standley's treatment included in his *Trees and Shrubs of Mexico* (1926). As a result of field work associated with several floristic projects and the efforts of numerous individual collectors, the number of collections of Mexican Acanthaceae has greatly increased during the five decades since Standley's flora was published. However, there have been no comprehensive studies of *Holographis* or of the genera here considered congeneric with it. Work on these genera has been limited to regional floristic treatments and descriptions of new taxa.

In the present treatment, the relationships of two genera recognized by Standley and subsequent workers and a third, more recently described genus are discussed. Both *Berginia* Harvey ex Bentham & Hooker and *Lundellia* Leonard are considered to be congeneric with the older genus *Holographis* Nees. In addition to the new combinations in *Holographis*, three species from Mexico are described as new to science. This study also presents information on aspects of the ecogeography and phenology of the species.

Holographis comprises ten species of shrubby perennials that are confined to arid and semiarid habitats in Mexico. Most species are restricted in their distribution and are known from relatively few collections. The genus is characterized by the following combination of characters: spicate inflorescences, a five-parted calyx, a relatively small, strongly zygomorphic corolla, four monothecous stamens of approximately equal length, pubescent thecae that lack any appendages, a short staminode, and an ellipsoid capsule bearing four seeds. In addition, the plants lack cystoliths, and all but three of the species have whorled leaves.

TAXONOMIC HISTORY AND INTRAFAMILIAL RELATIONSHIPS

Based on a Mexican collection of Ehrenberg, Nees described the genus *Holographis* and the species *H. ehrenbergiana* Nees in the supplement to his treatment of the Acanthaceae in De Candolle's *Prodromus* (1847). He placed the genus in tribe Gendarusseae subtribe Gendarusseae "section" Pseudo-Apelandreae and noted affinities with *Hemigraphis* Nees. Bentham and Hooker (1876) described the genus *Berginia* based on a Coulter collection from North America. The genus was placed in tribe Justicieae subtribe Asystasiaeae, and affinities with *Stenandrium* Nees were noted. Bentham and Hooker did not see any material of *Holographis*, but based on Nees's description they included that genus in tribe Justicieae subtribe Eujusticieae, where it was grouped with

Aphelandra R. Br. and *Geissomeria* Lindley. In 1885 Asa Gray described *Pringleophytum* A. Gray from a Pringle collection from Sonora, Mexico, noting an alliance between his genus and *Holographis*. Brandegee (1889) suggested that *P. lanceolatum* A. Gray and *B. virgata* Harvey ex Bentham & Hooker were conspecific. Rose (in Vasey & Rose, 1890) described a second species of *Berginia*, *B. palmeri* Rose, and confirmed Brandegee's notion that *P. lanceolatum* and *B. virgata* were the same species. Lindau (1895) provided accounts of both *Holographis* and *Berginia* in his influential treatment of the family in *Die Natürlichen Pflanzenfamilien*. He placed both genera in subfam. Acanthoideae tribe Aphelandreae, which included members of the family that have a corolla imbricate in bud and with an upper lip, an androecium consisting of four monothecous stamens, and typical Spaltenpollen. *Holographis* and *Neriacanthus* Bentham were distinguished from other genera of the Aphelandreae (including *Berginia*) largely by the presence of a staminode. *Berginia* was also reported to have an unusual pollen type with three pores, each flanked by two furrows. Lindau's conception of *Berginia* was probably based on a misidentified specimen, since the genus has a staminode and tricolpate pollen.

In 1906 Brandegee described an unusual plant from the Chihuahuan Desert as *Holographis ilicifolia* Brandegee, but he was uncertain of its generic position. Subsequently, two additional species of *Holographis* (*H. pallida* Leonard & Gentry and *H. parayana* Miranda) and a species and a variety of *Berginia* (*B. hintonii* Leonard and *B. virgata* var. *glandulifera* Leonard & Morton) have been described. Leonard and Gentry (in Gentry, 1948) noted that *H. pallida* might eventually prove worthy of generic status due to the apparent uniqueness of its connivent anthers. They also noted the similarity of this species to species of *Berginia* and doubted whether the two genera could be kept separate. In 1959 Leonard described the genus *Lundellia* from southwestern Mexico. He claimed that its closest affinity was with the large American genus *Aphelandra*.

Bremekamp (1965) suggested revisions of tribes and subtribes within the family. Although he did not list the genera that comprise his subfamilies and tribes, if one uses his scheme, the species under consideration in this study would be included in subfam. Acanthoideae tribe Aphelandreae, which contains members of the family having four monothecous stamens, two ovules per ovary cell, a distinctly bilabiate corolla, and prolate, tricolpate pollen (except in *Stenandrium* subg. SPHAEROSTENANDRIUM), but lacking cystoliths. According to Bremekamp, this tribe is confined to the neotropics.

The closest relatives of *Holographis*, and the only other members of Lindau's Aphelandreae that occur in Mexico, are *Stenandrium* and *Aphelandra*. In Mexico these three genera can be distinguished by the following key:

1. Corolla subactinomorphic, lobes homomorphic; plants often acaulescent. *Stenandrium*.
1. Corolla strongly bilabiate, lobes heteromorphic; plants rarely acaulescent.
 2. Corolla orange, red, or purple (yellow in *A. verticillata*), 30–70 mm long. *Aphelandra*.
 2. Corolla yellow, pink, rose-purple, or white, 7–18 mm long. *Holographis*.

Holographis appears to be rather closely related to *Aphelandra*. There is no known substantial morphological character that invariably separates them.

Indeed, the two genera show some of the same trends (e.g., whorled leaves and spinose-toothed laminae), although they are usually readily distinguishable by a suite of characters. In *Aphelandra* the bracts are often brightly colored, the length of the corolla can reach 75 mm, and a staminode is rarely present (Wasshausen, 1975). In addition, *Aphelandra* is primarily a genus of damp habitats, with a center of diversity in South America. Only ten species are known to occur in Mexico (Wasshausen, 1975), and these are largely restricted to the wetter habitats in the southern part of the country. In contrast, *Holographis* does not have colored bracts, the length of the corolla reaches only 18 mm, and a staminode is always present. The plants are restricted to Mexico, where they occur in arid and semiarid associations throughout the country.

It is tempting to suggest that *Holographis* represents an evolutionarily specialized line (adapted for the northern desert regions into which it radiated) of some part of the large and variable genus *Aphelandra* or its ancestor. Some of the differences between the genera may have arisen in response to (or may be maintained because of) the apparent differences in pollination mechanisms. The small, usually pale-colored flowers that contain little nectar (as observed in *H. ilicifolia* and *H. argyrea*) suggest that *Holographis* is pollinated by a small bee or a fly. In contrast, the large, nectar-yielding, usually reddish flowers of *Aphelandra* are commonly hummingbird pollinated (Wasshausen, 1975).

MORPHOLOGY

HABIT. Plants of *Holographis* are erect, often intricately branched subshrubs or shrubs to 2 m tall, arising from a stout, woody base. Variation in habit due to exposure is particularly observable in specimens of *H. ilicifolia* and *H. ehrenbergiana*. Exposed or drought-induced forms tend to be compact shrubs with small leaves and close nodes.

STEMS. The epidermis of the persistent, woody stems frequently exfoliates in strips, exposing a whitish new surface. The younger stems are greenish or purplish to silvery white and are usually subquadrate in cross section. The surface is smooth, soon becoming conspicuously fluted, and is variably pubescent.

LEAVES. The leaves of *Holographis* are either opposite (subopposite in some individuals) or whorled, depending on the species. Seven species (*H. ilicifolia*, *H. ehrenbergiana*, *H. pueblensis*, *H. anisophylla*, *H. pallida*, *H. hintonii*, and *H. parayana*) have whorled leaves, with four at each node. *Holographis tamau-lipica*, *H. argyrea*, and *H. virgata* have opposite leaves. In *H. pueblensis* the lower leaves are sometimes opposite or subopposite, and the upper leaves are whorled. The leaves are sessile or petiolate, simple, and usually entire. The leaves of *H. ilicifolia* are unusual in their chartaceous texture and spinose-toothed margins. The lamina varies from lanceolate through ovate, elliptic, and orbicular to obovate and is 3–64 by 2–28 mm.

The venation of all species of *Holographis* except *H. ilicifolia* is brochidodromous; that of *H. ilicifolia* is craspedodromous. In his study of leaf architecture in the Acanthaceae, Sreemadhaven (1976) noted the occurrence of both of these

venation types in the Aphelandreae and considered pinnate craspedodromy to be derived from the pinnate-camptodromous condition.

The leaves tend to have trichomes similar to those of the stem from which they arise, but dendroid trichomes are present on the unfolding leaves of *Holographis argyrea*.

VESTITURE. *Holographis* has both glandular and eglandular trichomes. The latter are more common, and when glandular trichomes occur, they are usually intermixed with eglandular ones. Trichomes of the vegetative axes are eglandular, 0.05–1 mm long, and erect to flexuose, retrorse, or ascendant. Depending on the species, the calyxes and the inflorescence axes, bracts, and bractlets can have glandular trichomes in addition to eglandular ones. The capitate glandular trichomes are 0.05–0.5 mm in length. Trichomes can also occur on most parts of the flowers, fruits, and seeds. Those of the seeds are unusual in being dendroid, often with circinate branches. Branched trichomes are not usually found on other parts of the plant.

INFLORESCENCES. The inflorescences are axillary or terminal bracteate spikes (usually reduced to two flowers in *Holographis ehrenbergiana*) to 15 cm long. The spikes are congested, erect, and relatively short (1–6 cm long) in most species, but they are often loose, lax, and longer in others (especially taxa in the *H. virgata* complex). The flowers are sessile in the axil of two isomorphic bractlets and a bract and are opposite (alternate in *H. ilicifolia*) at the nodes of the inflorescence axis.

FLOWERS. The calyx is gamosepalous, five parted, and radially symmetrical. The tube is shorter than the homomorphic lobes. The calyx is fairly constant in length within a species, and its outer surface is often glandular.

The corolla is gamopetalous, pentamerous, and bilaterally symmetrical. It varies from yellow and white to pinkish and purplish, often with colorful markings. The orientation of the corolla varies from horizontal (e.g., in *Holographis pallida*, *H. parayana*, and *H. tamaulipica*) to erect (e.g., in *H. pueblensis*, *H. argyrea*, and *H. ehrenbergiana*). The tube is usually shorter than the limb and is slightly ampliate toward the apex (except in *H. argyrea*). The limb is bilabiate, the upper lip with two petal lobes that are fused for most or all of their length, and the lower lip with three large, basally fused lobes. Two prominent ridges are often evident in the center of the lower lip. In bud the petal lobes are imbricate, with the upper lip innermost, concealed by the lateral and central lobes of the lower lip; the lower-central lobe is outermost. The corollas of most species have eglandular trichomes on the outer surface, but those of *H. parayana*, *H. anisophylla*, and *H. hintonii* have glands as well. The corolla of *H. anisophylla* is somewhat unusual in having glands on the inner as well as the outer surface; that of *H. tamaulipica* is glabrous on the outer surface, with the inner surface usually conspicuously pubescent along the central lobe of the lower lip and/or near the junction of the corolla and the filaments.

The androecium consists of four epipetalous stamens and a staminode. The staminode is a short, filamentlike projection arising on the dorsal side of the corolla between the posterior pair of stamens; it lacks a theca, may be either glabrous or pubescent, and is 0.1–1.3 mm long. In most species the staminode

emerges from the corolla at or about the same position as the filaments, although in *Holographis ilicifolia* it arises from the corolla up to 2 mm above the insertion of the filaments. The filaments of the fertile stamens emerge from the corolla near the apex of the tube and are either glabrous or pubescent. The anthers are monothealous and pubescent. The four thecae are frequently connivent at their apices and are basally rounded, lacking any appendages.

Pollen of at least one individual of each species (except *Holographis anisophylla*) was examined with a scanning electron microscope and/or a light microscope for shape, size, and sculpturing. Fresh pollen grains are prolate and generally uniform in size, with polar diameter (27.5–)35–40(–45) μm and equatorial diameter (17.5–)22.5–27.5(–30) μm . The grains are 1.3 to 1.6 times longer than wide. FIGURE 1 illustrates some of the variation in pollen of species of *Holographis*. The micrographs show that the grains are tricolpate. The colpi are often bifurcate near the poles, and the bifurcations from each colpus can fuse with those of the other colpi below the poles.

The gynoecium consists of a bicarpellate, superior ovary, a compound style, and usually two short stigma lobes. The ovary sits on a cuplike, fleshy disc. The style is filiform for most of its length but is conspicuously flared near the apex in some species. The presence or absence of trichomes on the style is usually constant for a species, but the styles of *Holographis pallida* and *H. virgata* can be either glabrous or pubescent. The stigma is either distinctly or inconspicuously bilobed, with the lobes often asymmetric.

FRUITS. The ovary develops into an indurate, two-valved capsule that dehisces explosively when mature. The capsule is ellipsoid in shape, splits to the base, and has no stalk; its outer surface is either glabrous or pubescent. The seed-bearing retinacula are hooklike and subequally inserted on the inner capsule wall. The seeds (up to four per capsule) are laterally flattened, suboval in shape, and either glabrous or pubescent. When present, the trichomes on the seeds are dendroid.

ECOGEOGRAPHY AND PHENOLOGY

Holographis is endemic to Mexico, from Baja California and northwestern Sonora, eastward to Tamaulipas, and southward to central Chiapas (MAPS 1, 3). Despite the extensive range of the genus in Mexico, most of the species have restricted distributions and are known from relatively few collections. *Holographis hintonii* and *H. anisophylla* are known only from the holotype, and *H. argyrea*, *H. tamaulipica*, and *H. pueblensis* are known from only two localities. *Holographis ehrenbergiana* and *H. virgata* have larger ranges, however, and can be common in certain regions.

There is no concentration of species in any one region of Mexico; in fact, the species are mostly allopatric, the only exceptions being *Holographis ehrenbergiana*, *H. tamaulipica*, and *H. pueblensis*, which overlap in range. There does appear to be a correlation of species with many of the arid and semiarid regions of Mexico, usually one species per region. *Holographis ilicifolia* is restricted to the Chihuahuan Desert, *H. virgata* to the Sonoran Desert region, *H. pallida* to the thorn forest south of the Sonoran Desert, *H. tamaulipica* to

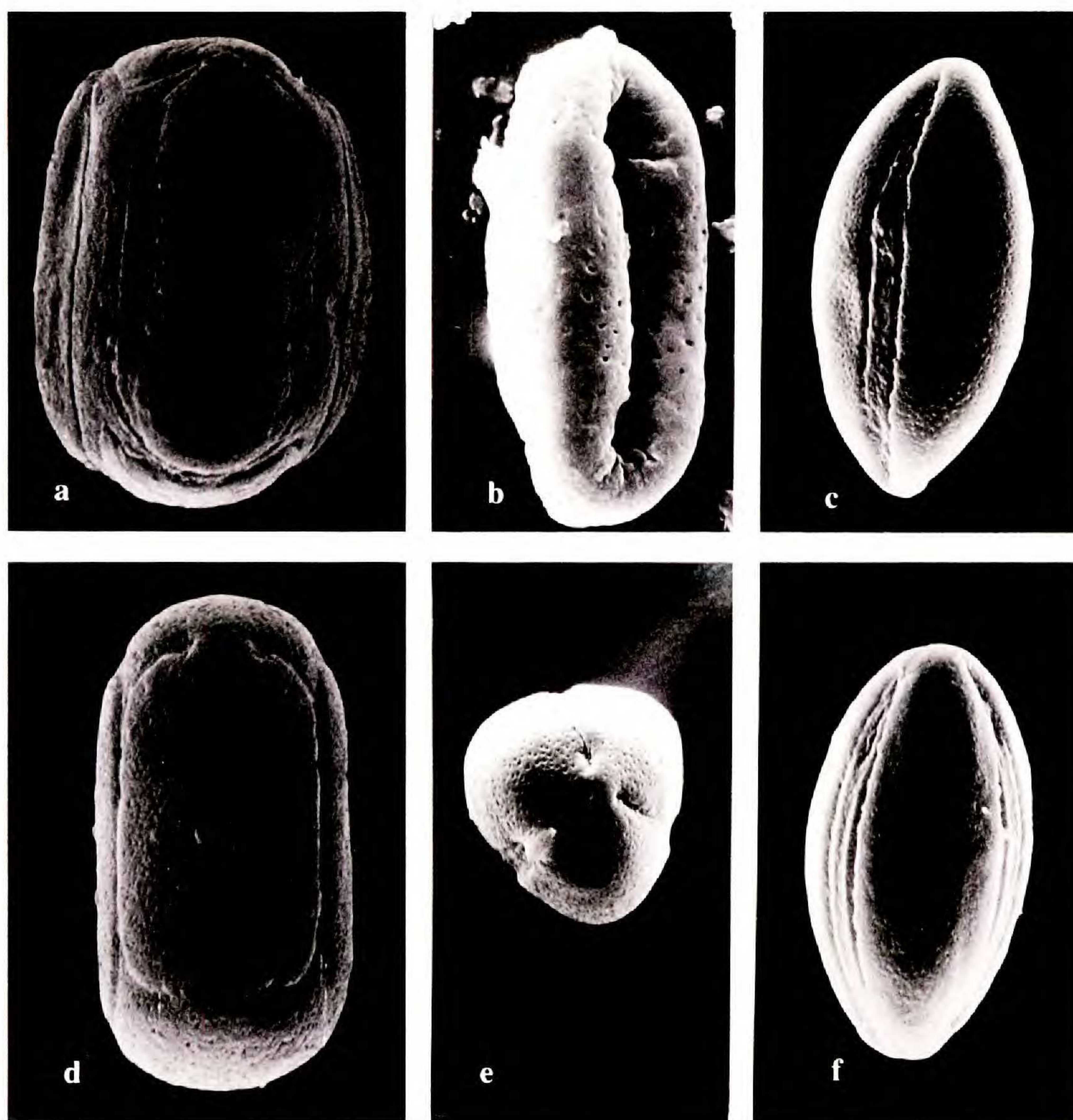
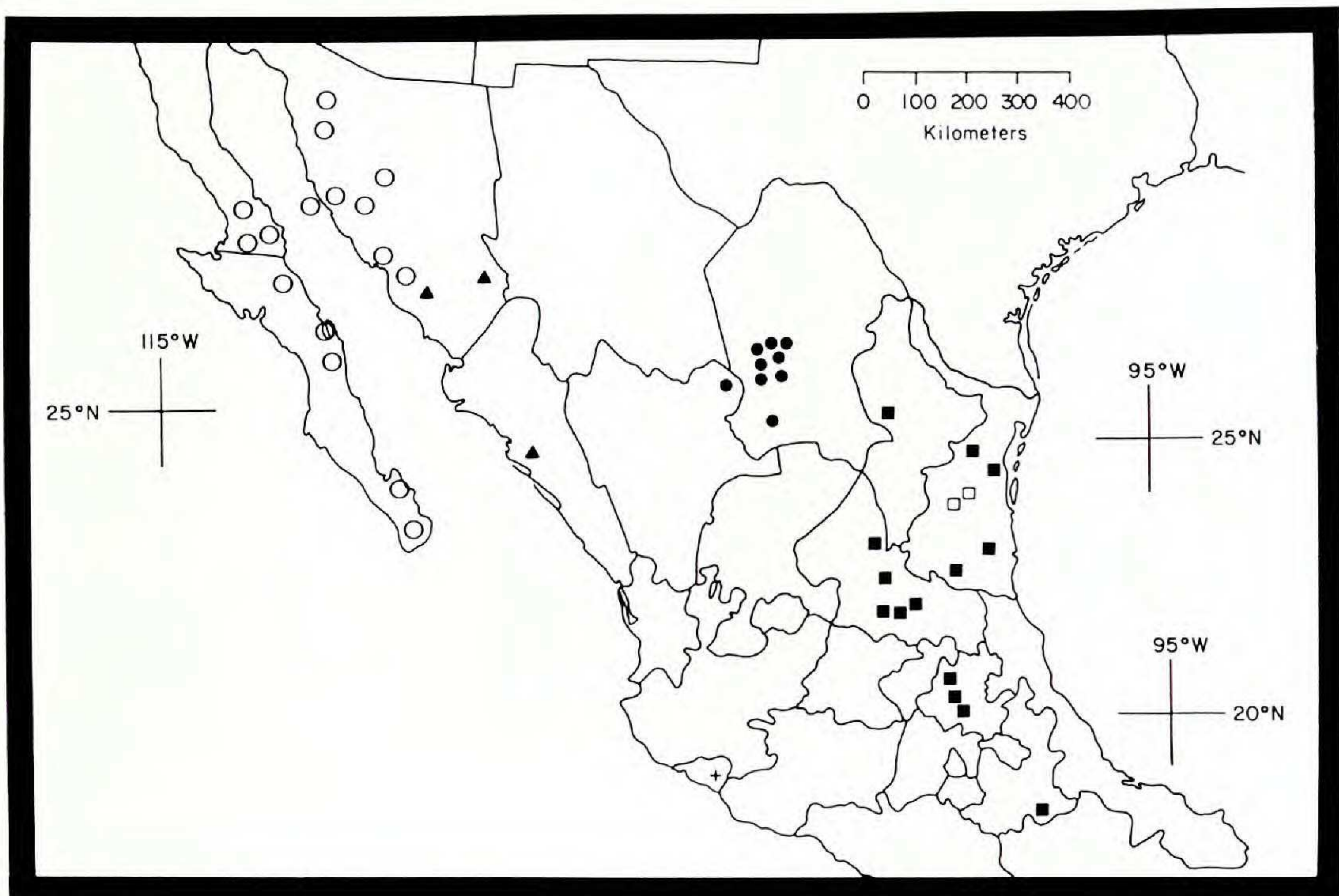


FIGURE 1. Variation in pollen of *Holographis* species: a, *H. virgata* subsp. *glandulifera* var. *glandulifera* (Moran 3928), equatorial view, $\times 775$; b, *H. argyrea* (T. Daniel 1242), equatorial view, $\times 900$; c, *H. ehrenbergiana* (González Quintero 3581), equatorial view, $\times 900$; d, *H. pallida* (H. Gentry 7022), equatorial view, $\times 775$; e, *H. ehrenbergiana* (González Quintero 3581), polar view, $\times 900$; f, *H. ehrenbergiana* (González Quintero 3581), equatorial view, $\times 900$.

the mesquite scrubland of central Tamaulipas, *H. pueblensis* to the arid Valley of Tehuacán, and *H. argyrea* and *H. hintonii* both to the arid tropical scrub of the Río Balsas Basin (however, their ranges are not known to overlap); *H. ehrenbergiana* is especially common in the Río Panuco relict desert region of Hidalgo but also occurs in the semiarid regions throughout northeastern Mexico. *Holographis parayana* and *H. anisophylla* both occur in regions of tropical deciduous forest that are somewhat isolated from the ranges of other species in the genus.

In his revision of the large genus *Aphelandra*, Wasshausen (1975) noted the pronounced endemism of many of the species and the wide scattering of individuals. *Holographis* appears to be closely related to *Aphelandra* (see discussion



MAP 1. Northern and central Mexico, showing distribution of *Holographis anisophylla* (plus sign), *H. ehrenbergiana* (solid squares), *H. ilicifolia* (solid dots), *H. pallida* (solid triangles), *H. tamaulipica* (open squares), and *H. virgata* (circles).

under Taxonomic History and Intrafamilial Relationships) and shows the same phenomena. Additional, local species of *Holographis* will undoubtedly be discovered as botanical exploration of Mexico continues.

The species occur in several habitats at elevations from near sea level to 2000 meters. The plants are generally found in arid and semiarid associations including desert scrub, thorn forest, and tropical deciduous forest. The most frequent habitats are on exposed rocky slopes and along gravelly washes and arroyos.

Only *Holographis ilicifolia*, *H. ehrenbergiana*, and *H. virgata* are known from sufficient collections to determine their flowering periodicity adequately. Although both *H. ilicifolia* and *H. ehrenbergiana* have been collected during most months of the year, the majority of specimens of each species were taken during the period from July through September, corresponding to the summer rainy season in the Chihuahuan Desert region and the dry regions of northeastern Mexico where these species occur. Members of the *H. virgata* complex have been collected in flower during every month except July, August, and September, although peak flowering occurs from March through May, corresponding to the end of the season of winter rains in the western section of the Sonoran Desert. The few collections of the other species of *Holographis* suggest that *H. pallida*, *H. hintonii*, *H. tamaulipica*, and *H. parayana* flower predominantly January through April, *H. pueblensis* in June and July, *H. argyrea* in October and November, and *H. anisophylla* in November and December.

Fruiting collections are not known for all of the species, and fruits and flowers are seldom found together on specimens of those species whose fruits are known. It appears that fruiting begins several weeks after flowering has started.

TAXONOMIC TREATMENT

Holographis Nees in DC. Prodr. **11**: 728. 1847. TYPE SPECIES: *Holographis ehrenbergiana* Nees.

Berginia Harvey ex Bentham & Hooker, Gen. Pl. **2**: 1096. 1876. TYPE SPECIES: *B. virgata* Harvey ex Bentham & Hooker.

Pringleophytum A. Gray, Proc. Amer. Acad. Arts **20**: 292. 1885. TYPE SPECIES: *P. lanceolatum* A. Gray.

Lundellia Leonard, Wrightia **2**: 1. 1959. TYPE SPECIES: *L. argyrea* Leonard.

Erect to spreading subshrubs to shrubs to 2 m tall, arising from stout, woody base. Older stems woody, pubescent, or glabrate; younger stems green, purplish, or silvery white, terete to quadrate to ellipsoid in cross section, the surface smooth to striate to fluted, pubescent, often densely so. Leaves opposite (rarely subopposite) or whorled (4 per node), sessile to petiolate; lamina linear-lanceolate to obovate, the margin entire (spinose toothed in *H. ilicifolia*), flat or revolute, the surfaces pubescent, often sparsely so, with abaxial surface punctate in some species. Inflorescences axillary or terminal spikes (usually reduced to 2 flowers in *H. ehrenbergiana*); flowers sessile, opposite (alternate in *H. ilicifolia*) along spike axis, subtended by 2 paired, isomorphic bractlets and a bract; bracts and bractlets usually similar in shape, often of different relative lengths. Calyx deeply 5-lobed, lobes homomorphic; corolla yellow or white to purplish or pinkish, bilabiate, pubescent (glabrous in *H. tamaulipica*) on outer surface, the tube usually shorter than the lips, usually ampliate above, the upper lip bilobed, the lower lip trilobed, with lobes spatulate, central lobe usually conspicuously larger and extending beyond lateral ones and usually with 2 prominent ridges down middle; stamens 4, included or slightly exserted and appressed to upper lip, the filaments glabrous or pubescent, the anthers monothealous, with thecae introrse, pubescent, often connivent; staminode short, borne between posterior pair of stamens, glabrous or pubescent, theca lacking; style terminal, filiform, glabrous or pubescent, either flared near apex into distinct, equal or unequal stigmatic lobes or slightly flared and with stigmatic lobes inconspicuous. Capsules brown, ellipsoid, bilocular, splitting to base, glabrous or pubescent on outer surface; retinacula 4 per capsule, hooklike. Seeds 4 per capsule (or fewer by abortion), laterally flattened, suboval, surface and margins glabrous or pubescent.

DISTRIBUTION. Mexico: Baja California Norte, Sonora, Coahuila, Nuevo León, and Tamaulipas, southward to Chiapas.

KEY TO THE SPECIES OF HOLOGRAPHIS

- 1. Leaves opposite (rarely subopposite).
 - 2. Cauline trichomes ascendant-appressed; inflorescence spikes axillary; bracts 2–3 mm long, glabrous; calyx 4–5 mm long; corolla glabrous on outer surface. 1. *H. tamaulipica*.
 - 2. Cauline trichomes straight, flexuose or retrorse; inflorescence spikes terminal on branches; bracts 3–8 mm long, pubescent; calyx 5–8 mm long; corolla pubescent on outer surface.

3. Cauline trichomes 0.05–1 mm long; corolla reddish pink, 9–14 mm long; stamens 2.8–5 mm long; Sonoran Desert region. 2. *H. virgata*.
3. Cauline trichomes 0.05 mm long or less; corolla yellow, 7–9.5 mm long; stamens 1.5 mm long; Guerrero. 3. *H. argyrea*.
1. Leaves whorled, 4 per node (lower leaves of *H. pueblensis* sometimes opposite to subopposite).
4. Leaves orbicular, 0.8–1.3 times longer than wide, margin spinose toothed; bracts alternate; Chihuahuan Desert region. 4. *H. ilicifolia*.
4. Leaves lanceolate to obovate, 1.5–4.5 times longer than wide, margin entire; bracts opposite; not of Chihuahuan Desert region.
5. Corolla 8–10 mm long, glandular on outer surface; stamens 2.5–3.5 mm long.
6. Cauline trichomes ascendant-appressed, 0.1–0.3 mm long; bracts triangular to lance-subulate, eglandular, emucronate; calyx 2–3 mm long; style 5–6 mm long; ovary glabrous. 5. *H. parayana*.
6. Cauline trichomes retrorse, 0.05–0.1 mm long; bracts lance-ovate to orbicular, glandular, mucronate; calyx 4–5 mm long; style 3.5–4 mm long; ovary pubescent.
7. Inflorescence axis glandular-pubescent with glandular trichomes 0.05 mm long and straight eglandular trichomes 0.05–0.1 mm long; bracts lance-ovate to ovate, 2.5–3 mm long; bractlets lance-ovate to ovate, 2–2.8 mm long; stamens 2.5–3 mm long; staminode pubescent. 6. *H. anisophylla*.
7. Inflorescence axis eglandular with crooked, interwoven trichomes to 0.8 mm long; bracts broadly ovate to orbicular, 1.5–2 mm long; bractlets lanceolate, 1.5–2 mm long; stamens 3–3.5 mm long; staminode glabrous. 7. *H. hintonii*.
5. Corolla 10–18 mm long, pubescent with eglandular trichomes on outer surface; stamens 3.5–11 mm long.
8. Cauline trichomes retrorse, 0.05–0.2 mm long; laminar margin flat; bracts mucronate; corolla white to lavender, 10–12 mm long, horizontal at anthesis; style 5.3–6 mm long. 8. *H. pallida*.
8. Cauline trichomes straight to ascendant-appressed, 0.1–0.7 mm long; laminar margin revolute; bracts emucronate; corolla yellow, 12–18 mm long, vertical at anthesis; style 12–16 mm long.
9. Inflorescence spikes many flowered, to 4.5 cm long; bracts 6.5–11 by 1.5–2 mm; calyx 7–10.5 mm long. 9. *H. pueblensis*.
9. Inflorescence spikes to 2 cm long, usually reduced to 2 flowers; bracts 1.5–5 by 0.5–1 mm; calyx 3.5–6 mm long. . . . 10. *H. ehrenbergiana*.

1. **Holographis tamaulipica** T. F. Daniel, sp. nov.

FIGURE 2.

Frutex erectus. Caules juniores substriati pubescentes trichomatibus eglandulosis 0.2–0.6 mm longis. Folia opposita; laminae lanci-ovatae vel ellipticae, (15–)25–64 mm longae, (6–)9–28 mm latae, 2–4-plo longiores quam latiores, marginibus revolutis ciliatis. Inflorescentia spicata; bractae triangulatae vel ovatae, 2–3 mm longae, 1.5–2 mm latae; bracteolae lanceolatae, 1.5–2.2 mm longae. Calyx 4–5 mm longus; corolla 9–11 mm longa, extus glabra; stamina 3.5–4 mm longa filamentis 2–2.5 mm longis, pubescentibus; staminodium 0.2–0.3 mm longum, pubescens; stylus 6–6.5 mm longus, glaber. Capsula 9 mm longa, glabra.

Erect shrub. Older stems pubescent or glabrate; younger stems green, terete in cross section, the surface somewhat striate, evenly pubescent, the trichomes

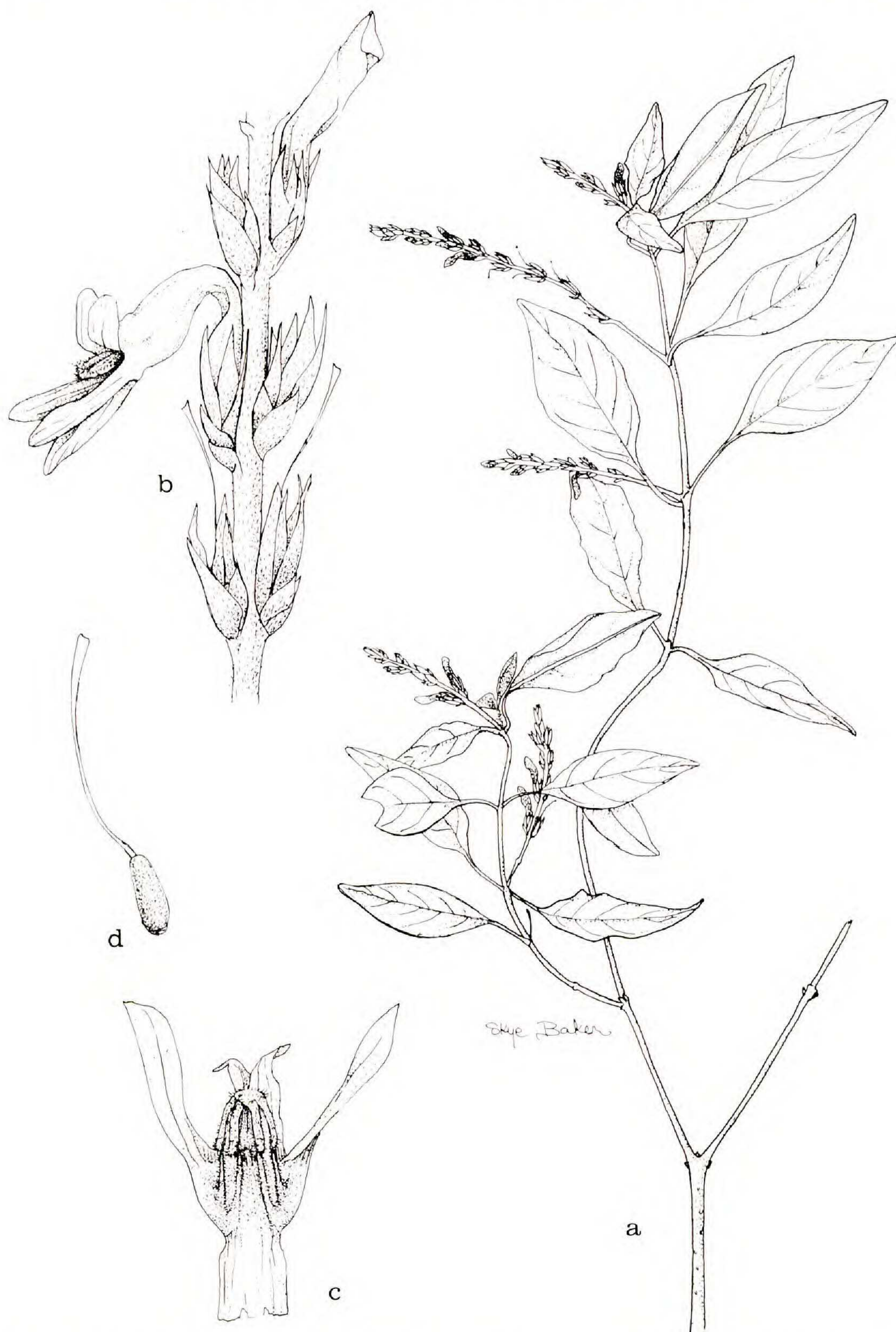


FIGURE 2. *Holographis tamaulipica* (from holotype): a, habit, $\times 0.6$; b, spike, $\times 3.5$; c, dissected flower, $\times 4$; d, gynoecium, $\times 4.5$.

eglandular, ascendant-appressed, 0.2–0.6 mm long. Leaves opposite, ascendant to horizontal; petiole to 10 mm long, pubescent; lamina lance-ovate to elliptic, attenuate at base, acute at apex, (15–)25–64 by (6–)9–28 mm, 2 to 4 times

longer than wide, the margin entire, revolute, ciliate with erect to flexuose trichomes 0.2–0.8 mm long, the surfaces subglabrous or sparsely pubescent. Inflorescences axillary or terminal, pedunculate spikes to 9 cm long; peduncles 1–9 mm long; axes pubescent with erect to ascendant trichomes 0.05–0.2 mm long; flowers opposite at spike nodes; lower bracts (rarely absent) sterile; upper bracts fertile, triangular to ovate, 2–3 by 1.5–2 mm, submucronate to mucronate at apex, outer surface glabrous, margin often ciliate; bractlets lanceolate, shorter than or approximately same length as subtending bract, 1.5–2.2 by 0.7–1 mm, pubescent like bracts. Calyx 4–5 mm long, the lobes lance-subulate, mucronate at apex, pubescent like bracts; corolla white (label data), horizontal at anthesis, 9–11 mm long, glabrous on outer surface, the tube 4–5 mm long, ampliate above, the upper lip 3.5–5 mm long, with lobes 2–3 mm long, the lower lip 5–6 mm long, with lobes spatulate, 3.5–4.5 by 1.5–2 mm; stamens 3.5–4 mm long, the filaments 2–2.5 mm long, pubescent, the thecae 1.5–2 mm long, pubescent; staminode 0.2–0.3 mm long, pubescent; style 6–6.5 mm long, glabrous, flared at apex, the stigma unequally bilobed, with longer lobe to 0.5 mm long. Capsules 9 mm long, 3.8 mm in diameter, glabrous. Seeds not seen.

TYPE. Mexico, Tamaulipas, vicinity of Victoria, ca. 320 m, 1 Feb.–9 April 1907, *Palmer 135* (holotype, GH!; isotype, F!).

This species is known only from the type specimens and one additional collection, both of which were collected near Victoria, Tamaulipas (MAP 1) in the early spring. The paratype was collected on a shaded limestone ledge in oak woods at 1200 meters.

Holographis tamaulipica is unique among the known species of *Holographis* in having a glabrous corolla. It does not appear to be very closely related to the other two species with opposite leaves. In cauline pubescence, flower size, and corolla orientation it resembles *H. parayana*.

ADDITIONAL SPECIMEN EXAMINED. **Mexico.** TAMAULIPAS: 12 mi from river at Victoria on road to Jamauve, *Moore & Valiente M. 6159A* (US).

2. *Holographis virgata* (Harvey ex Bentham & Hooker) T. F. Daniel, comb. nov.

Berginia virgata Harvey ex Bentham & Hooker, Gen. Pl. 2: 1097. 1876. TYPE: "California incola," without date, *Coulter 603* (holotype, K!; isotypes, GH!, K (2 sheets)!). *Pringleophytum lanceolatum* A. Gray, Proc. Amer. Acad. Arts 20: 293. 1885. TYPE: Mexico, Sonora, rocky hills 50 mi below Altar and 30 mi from Gulf of California, 1884, *Pringle s.n.* (holotype, GH; isotypes, F!, NY!, US!).

Erect shrub to 2 m tall. Older stems often whitish, pubescent or glabrate; younger stems pale green, soon becoming either whitish or purplish, subquadrate to quadrate in cross section, the surface striate, soon becoming conspicuously fluted, evenly pubescent, with trichomes eglandular and erect, flexuose, or retrorse, 0.05–0.7(–1) mm long. Leaves opposite (or subopposite), ascendant, sessile to petiolate; petiole (if present) to 5 mm long, pubescent; lamina linear-lanceolate to obovate, acute to attenuate at base, acute to rounded (rarely emarginate) at apex, (4–)6–46 by 2–26 mm, 1.1 to 9.2 (to 17) times longer than

wide, the margin entire, flat to revolute, ciliate, the surfaces pubescent. Inflorescences terminal, loosely or densely bracteate spikes to 15 cm long; axes pubescent with eglandular trichomes or with mixture of eglandular and glandular trichomes; flowers opposite (to subopposite) at spike nodes; lower bracts (up to 6 series) often sterile, triangular to orbicular; upper bracts fertile, somewhat foliaceous, lance-ovate to ovate to elliptic to orbicular, 3–8 by 1.5–5 mm, usually pubescent like inflorescence axis; bractlets lance-subulate to linear to lanceolate, approximately equal to or shorter than subtending bract, 2–6 by 0.6–1.5 mm, pubescent with eglandular or mixture of eglandular and glandular trichomes. Calyx 5–8 mm long, the lobes lanceolate or oblanceolate, pubescent like bractlets; corolla reddish pink with white markings, 9–14 mm long, pubescent on outer surface with eglandular trichomes (rarely with glandular trichomes as well in subsp. *glandulifera* var. *glandulifera*), the tube 5–8 mm long, ampliate above, the upper lip (2.5–)3–5 mm long, with lobes 1.5–4 mm long, the lower lip 4–8 mm long, with lobes spatulate, 2.5–6 by 1.5–3.5 mm; stamens 2.8–5 mm long, the filaments 1.5–4 mm long, pubescent or nearly glabrous, the thecae 1.6–2.5 mm long, pubescent (anterior pair usually more densely so); staminode 0.5–0.8 mm long; style 5–7 mm long, glabrous or pubescent, flared at apex, the stigma subequally bilobed, 0.3–0.5 mm long. Capsules 7–12 mm long, 3–5 mm in diameter, pubescent or essentially glabrous, with trichomes often restricted to apex, eglandular, 0.05–0.3 mm long, the retinacula 1.5–2.5 mm long. Seeds obliquely cordate to widely elliptic, 2–3.5 by 2–3 mm, pubescent with dendroid trichomes to 0.3 mm long.

As treated in this study, *Holographis virgata* comprises three taxa formerly recognized in *Berginia*. The most perplexing problem remaining in *Holographis* is the status of these taxa from Baja California and Sonora. The geographic discontinuity between the eglandular northern populations and the glandular southern populations justifies their recognition at the rank of subspecies. Due to minor differences in pubescence and an apparent difference in habitat elevation among the southern populations, two varieties are recognized in the southern subspecies. I feel confident that these plants are all part of the same species. The infraspecific treatment presented here, however, may presuppose a greater degree of understanding of this complex than can be obtained from herbarium material alone. Although the differences in pubescence among the three taxa are clear and most specimens can be easily identified, the nature of these distinctions is subtle. Pubescence can be influenced by environmental factors. Field work in Baja California and cultivation of these plants in an experimental garden will undoubtedly increase our understanding of their relationships.

Key to the Infraspecific Taxa of *Holographis virgata*

1. Inflorescence axes, bracts, bractlets, and calyx eglandular (rarely with inconspicuous glands on bractlets and calyx); bractlets 0.6–1 mm wide; Sonora and Baja California north of lat. 28°N. 2a. *H. virgata* subsp. *virgata*.
1. Inflorescence axes, bracts, bractlets, and calyx conspicuously glandular; bractlets 1–1.5 mm wide; Baja California, mostly south of lat. 28°N.

2. Leaves and young stems scaberulous, with trichomes retrorse, 0.05–0.1 mm long; usually below 600 m alt. 2b. *H. virgata* subsp. *glandulifera* var. *glandulifera*.
2. Leaves and young stems hirtellous, with trichomes straight to flexuose, 0.1–1 mm long; usually above 600 m alt. 2c. *H. virgata* subsp. *glandulifera* var. *palmeri*.

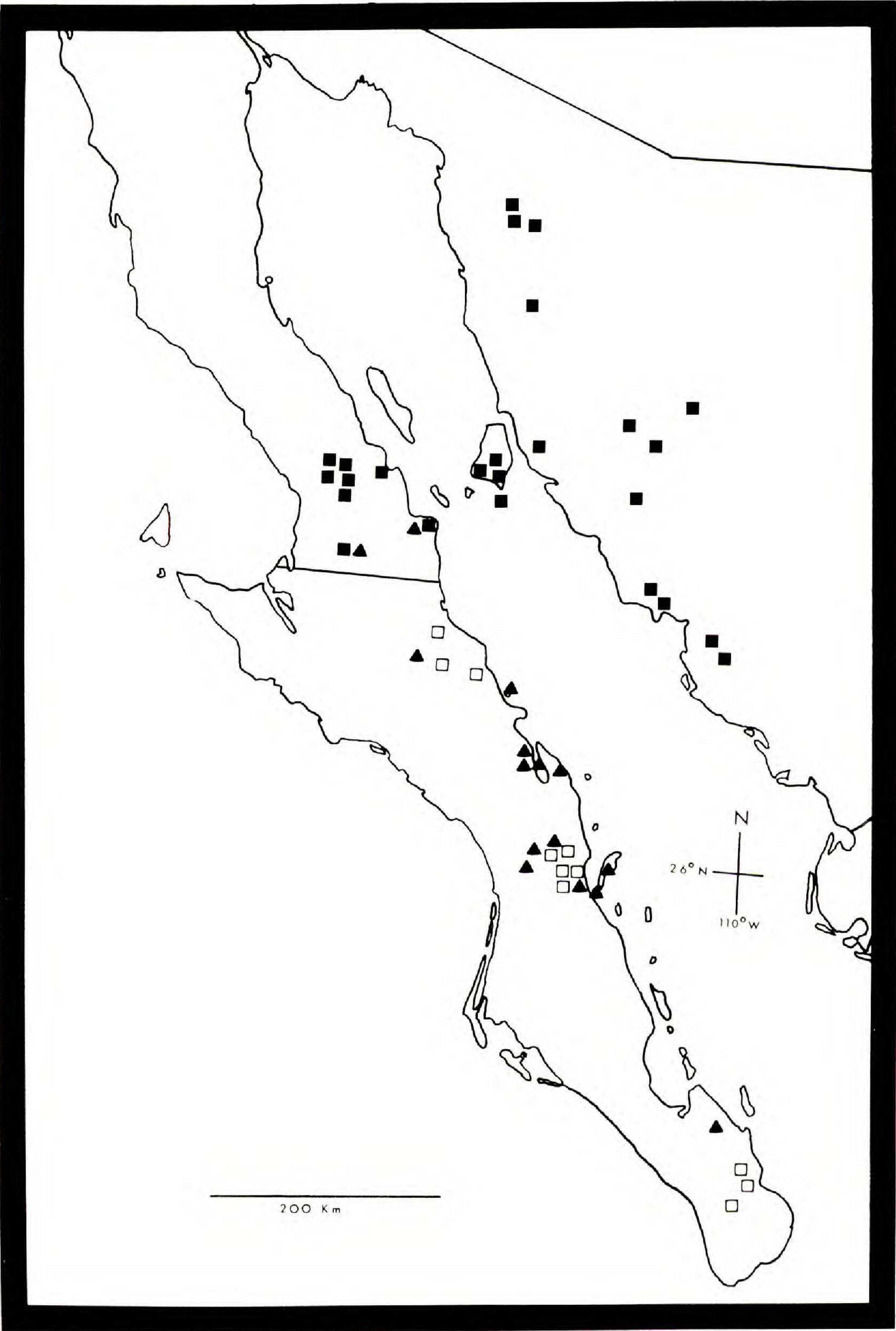
2a. *Holographis virgata* (Harvey ex Bentham & Hooker) T. F. Daniel subsp. *virgata*

Trichomes of younger stems erect to retrorse, 0.05–0.1 mm long. Leaves sessile or subsessile; lamina linear-lanceolate to lanceolate to elliptic (to obovate), (4–)7–43 by 2–9(–14) mm, (1.6 to) 3 to 17 times longer than wide. Inflorescence axes pubescent with eglandular, erect to retrorse trichomes 0.05–0.2(–0.5) mm long; bracts 1.5–3 mm wide, pubescent like inflorescence axis; bractlets 0.6–1 mm wide, pubescent like bracts (rarely also with scattered glandular trichomes to 0.2 mm long). Lower lip of corolla 5–8 mm long, lobes 4–6 by 2.5–3.5 mm. Capsule essentially glabrous to pubescent, trichomes often restricted to apex.

DISTRIBUTION AND HABITATS. Sonoran Desert of western and central Sonora and southern Baja California Norte (MAP 2); on gravelly slopes and along arroyos and washes, 15–1300 m alt.; with species of *Jatropha* L., *Pachycereus* (A. Berger) Britton & Rose, *Pachycormus* Cov. ex Standley, *Idria* Kellogg, *Larrea* Cav., *Opuntia* Miller, *Acacia* Miller, *Cercidium* Tulasne, *Simmondsia* Nutt., *Croton* L., and *Carnegiea* Britton & Rose.

FLOWERING AND FRUITING. Flowering October through June; fruiting simultaneously, more commonly during latter portion of flowering period.

REPRESENTATIVE SPECIMENS. **Mexico.** BAJA CALIFORNIA NORTE: Mina Desengaña, ca. 16 mi N of Punta Prieta, *H. Gentry & Cech* 8887 (MEXU, MICH, US); ca. 22 mi from Bahía Los Angeles on road to San Borja, *H. Gentry & McGill* 23313 (ASU, DES, MICH); 7 mi W of San Francisquito Bay, *Harbison* 41665 (SD); Las Animas Bay, *I. Johnston* 3509 (CAS, GH, NY, UC); Paredones, *Montufar* 42 (ENCB); Agua de Higuera, *Moran* 7956 (ARIZ, DS, MICH, SD, UC); Sierra San Borja, San Juan Mine, *Moran* 8060 (DS, SD, UC); Turners Is., *Moran* 13024 (SD, UC); Calmallí, *Purpus* 56 (DS, F, NY, UC, US); 8 mi N of Mission San Borja, *Thorne & Henrickson* 32677 (MICH); 3 mi S of Agua Higuera along road to Mission San Borja, *Wiggins & Wiggins* 14830 (CAS, MEXU, MICH). SONORA: 12 mi NW of Hermosillo, *Abrams* 13305 (DS, F); canyon back of Palma, 40 mi S of Hermosillo, *Abrams* 13348 (DS); ca. 31 mi E of Punta Cirio between Puerto Libertad and Caborca, *Bowers & McLaughlin s.n.*, 13 April 1979 (ARIZ); 10 mi NW of Hermosillo, *C. Carter s.n.*, 13 April 1932 (MICH); near Guaymas, *Dawson* 1075 (F, MICH); San Miguel de Horcasitas, *Eisen s.n.*, May 1892 (US); Picu Mts., Altar Distr., *H. Gentry* 4479 (DES, MICH, MO); Sierra Cajon del Diable, *H. Gentry* 11622 (MEXU, MICH); 22.2 mi N of Bahía Kino Nuevo, *Hastings & Turner* 64-40 (ARIZ, DS, SD); 0.9 mi E of Pitiquito, *Hastings & Turner* 64-58 (ARIZ, DS, SD); Guaymas, *I. Johnston* 3114 (CAS, GH, US); Hermosillo, *Jones* 22531 (MO); 8 mi NW of Caborca on road to Tajitos, *Keck* 4059 (CAS, DS, F, MO, NY); near Pozo Cerna, *Long* 62 (US); Tiburón Is., *Moran* 4065 (DS, SD, UC); Guaymas, *Palmer* 307 (GH); near Rancho Verruga, Distr. Altar, *Shreve* 5823 (ARIZ, US); 15 mi NW of Caborca, *Shreve* 7553 (ARIZ, F, MICH, MO, US); ca. 20 mi NE of Obregón, *Spaulding* 75-3-12 (ARIZ); 8 mi ESE of Vicam along Hwy. 15, *Turner & Hastings* 69-64 (ARIZ); 0.2 mi W of Rancho San Alfroso, *Turner & Duek* 79-37 (ARIZ); Puerto Los Mochos, Rancho Los Mochos, 20.7 mi NE of Desemboque de San Ignacio, *Van Devender & Kearns s.n.*, 17 Feb. 1977 (ARIZ).



MAP 2. Northwestern Mexico, showing distribution of infraspecific taxa of *Holographis virgata*: subsp. *virgata* (solid squares), subsp. *glandulifera* var. *glandulifera* (solid triangles), subsp. *glandulifera* var. *palmeri* (open squares).

This is the most widely distributed and most variable subspecies of *Holographis virgata*. It occurs primarily to the north and east of the range of *H. virgata* subsp. *glandulifera*, but the two subspecies do come together in southern Baja California Norte near Calmallí (lat. 28°08'N, long. 113°24'W). At this locality Purpus collected specimens of *H. virgata* subsp. *virgata*, *H. virgata* subsp. *glandulifera* var. *glandulifera*, and intermediates. The intermediate plants on Purpus 56 (UC) have sparsely glandular inflorescence axes, while other plants on the sheet have densely glandular (*H. virgata* subsp. *glandulifera* var. *glandulifera*) and eglandular (*H. virgata* subsp. *virgata*) axes. Duplicates of Purpus's collection at F and NY contain plants with varying degrees of glandularity. *Brandegee 443* from the Sierra de la Laguna in the Cape Region of Baja California Sur contains sprigs of *H. virgata* subsp. *virgata* and of *H. virgata* subsp. *glandulifera* var. *palmeri*. Although there is some variation among the sprigs of *H. virgata* subsp. *virgata* in the length of the pubescence on the inflorescences, the variation falls within the range normally encountered in that subspecies.

Annetta Carter, of the University of California (Berkeley) Herbarium, notes (*in litt.*) that during Brandegee's trip from Magdalena Bay to San Quintín in 1889, he was in the vicinity of Calmallí in late April. This was the only time he passed through the range of *Holographis virgata* subsp. *virgata*. She notes that at that time, Brandegee could have collected the material of *H. virgata* subsp. *virgata* as represented on *Brandegee 443*. While working on his collections of 1889 and 1890, he might have mixed material of the two subspecies.

Holographis virgata subsp. *virgata* shows considerable variation in the length of the eglandular pubescence on the inflorescence axes and in the amount of pubescence on the capsules. It can be distinguished from *H. virgata* subsp. *glandulifera* by the general absence of glandular trichomes on the inflorescence; however, in some individuals the bractlets and calyx can contain inconspicuous glands.

2b. *Holographis virgata* subsp. *glandulifera* (Leonard & Morton) T. F. Daniel, comb. et stat. nov., var. *glandulifera*

Berginia virgata var. *glandulifera* Leonard & Morton, Contr. Dudley Herb. 4: 24. 1950. TYPE: Mexico, Baja California Sur, 32 mi S of Mulegé, 15 March 1935, Shreve 7101 (holotype, US!; isotypes, ARIZ!, DS!, F!, MICH!).

Trichomes of the younger stems retrorse, 0.05–0.1 mm long. Leaves sessile; petiole to 3 mm long; lamina lance-ovate to oblanceolate, 6–43 by 3–22 mm, 1.3 to 3.8 times longer than wide. Inflorescence axes pubescent with mixture of glandular and eglandular trichomes, the former 0.1–0.3 mm long, the latter erect to flexuose, 0.05–0.3 mm long; bracts (2–)2.5–5 mm wide, lower ones pubescent like leaves, upper ones pubescent like inflorescence axis; bractlets 1–1.5 mm wide, pubescent like inflorescence axis but usually with more numerous glands. Lower lip of corolla 4–5 mm long, lobes 3–4 by 1.5–3 mm. Capsules pubescent.

DISTRIBUTION AND HABITAT. Known from southern Baja California Norte, but more common in eastern and central Baja California Sur (MAP 2); rocky slopes,

arroyos, and gravelly washes to about 600 m alt.; with *Lysiloma* Benth., *Mimosa* L., *Jatropha*, *Bursera* Jacq. ex L., *Pachycereus*, *Lemaireocereus* Britton & Rose, *Ruellia* L., *Fouquieria* Kunth, and *Cyrtocarpa* Kunth.

FLOWERING AND FRUITING. Flowering November through May and into June; fruiting simultaneously, more commonly during latter portion of flowering season.

REPRESENTATIVE SPECIMENS. **Mexico.** BAJA CALIFORNIA NORTE: 20 mi W of Bahía San Francisquito, *Humphrey 6830a* (ARIZ); diggings at Calmallí, *Purpus 56, pro parte* (UC). BAJA CALIFORNIA SUR: Purísima to Comondú, *Brandegees n.*, 15 Feb. 1889 (UC); Comondú, *Brandegees n.*, 15 Feb. 1890 (F, GH); 12.4 km SE of La Paz on road to Los Planes, *A. Carter 2625* (DS, MEXU, MICH, SD, UC, US); vic. of Rancho Los Burros, E of Llanos de San Pedro, NE of Comondú, *A. Carter & Ferris 3430* (DS, MEXU, SD, UC); Arroyo Carrizal, E of Rancho El Horno (NE of San Xavier), *A. Carter & Ferris 3829a* (CAS, UC); S of Tinaja de Naucajoa, Cerros de Naucajoa (W of Llanos de San Juan), *A. Carter 4502* (UC); Puerto Escondido, *Dawson 1098* (F, MICH); Las Cuevitas below Comondú, *H. Gentry 4235* (DES, DS, MICH, MO); between San Ignacio and Los Martiles, *H. Gentry 7872* (ARIZ, DS, MICH, UC); San Nicholas Bay, *I. Johnston 3729* (CAS); Carmen Is., Puerto Ballandra, *I. Johnston 3820* (CAS, GH, NY, UC, US); Carmen Is., Ballandra Bay, *Moran 3928* (DS, SD, UC, US); San Marcos Is., Arroyo de los Chivos, *Moran 8999* (SD); Danzante Is., *Moran 9249* (SD); island in Conception Bay, *Rempel 197* (ARIZ), *208* (ARIZ); 14 mi S of Mulegé, *Shreve 7086* (ARIZ, F, GH, MICH, MO).

This variety resembles *Holographis virgata* subsp. *virgata* in the pubescence of the vegetative axis, and where the ranges of these taxa overlap, intermediates occur. In its distribution and in characters of inflorescence pubescence and bract width, this variety appears closer to *H. virgata* subsp. *glandulifera* var. *palmeri*. These latter taxa are distinguishable from each other by the relative lengths of the foliar and cauline trichomes and by the differences in elevation of their habitats.

2c. ***Holographis virgata* subsp. *glandulifera* var. *palmeri*** (Rose) T. F. Daniel, comb. et stat. nov.

Berginia palmeri Rose, Contr. U. S. Natl. Herb. **1**: 86. 1890. TYPE: Mexico, Baja California Sur, Santa Rosalía, 15 March 1890, *Palmer 272* (holotype, US!; isotypes, A!, DS!, F!, GH!, NY!).

Trichomes of the younger stems erect to flexuose, 0.1–0.7(–1) mm long. Leaves sessile to petiolate; petiole to 5 mm long; lamina lance-ovate to obovate, (6–)11–46 by (4–)7–26 mm, 1.1 to 3.3 times longer than wide. Inflorescence axes pubescent with mixture of eglandular and glandular trichomes, the former 0.2–1 mm long, the latter 0.2–0.5 mm long; bracts 2.5–4.5 mm wide, pubescent like inflorescence axis; bractlets 1–1.5 mm wide, pubescent like inflorescence axis although glandular trichomes usually more numerous. Lower lip of corolla 5–6.5 mm long, lobes 2.5–4 by 2–3 mm. Capsules pubescent.

DISTRIBUTION AND HABITAT. Eastern Baja California Sur (especially common in and around Sierra de la Giganta (MAP 2)); among rocks on slopes and in arroyos above 600 m alt.; with *Jatropha*, *Hechtia* Klotzsch, *Pachycormus*, *Franseria* Cav., *Lysiloma*, *Lemaireocereus*, *Colubrina* Rich. ex Brongn., *Bur-*

sera, *Ficus* L., *Erythrina* L., *Agave* L., *Bernardia* Miller, *Viguiera* Kunth, and *Croton*.

FLOWERING AND FRUITING. Flowering October through June; fruiting predominantly March through June.

REPRESENTATIVE SPECIMENS. **Mexico.** BAJA CALIFORNIA SUR: Sierra de Laguna, *Brandege* 443 (UC); Arroyo Carrizal, E of Rancho El Horno (NE of San Xavier), *A. Carter & Ferris* 3819, *pro parte* (CAS, MEXU, UC, US); N slope of Pílon de las Parras, W of Loreto, *A. Carter & Sharsmith* 4215 (CAS, F, MO, NY, UC, US); Sierra de la Giganta, S of La Puerta, W end of Valle de los Encinos (S side of Cerro Giganta), *A. Carter & Reese* 4574 (CAS, MEXU, UC, US); Sierra de la Giganta, Mesa de San Geronimo, N of Rancho Viejo, *A. Carter* 5131 (CAS, GH, MICH, SD, UC, US); 5 mi S of San Bartolo, *Gallagher* 139 (ASU); Sierra Giganta above Pto. Escondido, *H. Gentry* 3762 (A, ARIZ, DES, MICH, MO, UC); Volcán las Tres Vírgenes, *Moran* 20459 (SD); La Ciénega Arroyo, Distr. of Buena Vista, *Peters* 206 (UC); 8 mi E of pass of Tres Vírgenes Peak, *Shreve* 7051a (ARIZ); El Purgatorio grade W of Santa Rosalía, *Wiggins & Wiggins* 18206 (CAS, DS, MEXU).

Most (if not all) of the specimens from the vicinity of the Sierra de la Giganta were collected above 600 meters in elevation; however, *Peters* 206 (from the Cape Region) was collected at about 33 m alt. Ms Carter notes (*in litt.*), "In the Cape Region, some plants occur both at low and higher altitudes whereas to the north (Sierra de la Giganta) the same taxon is restricted to higher altitudes. A case in point is *Jatropha vernicosa* which occurs above 2000 feet in the Sierra de la Giganta, but in the Cape Region it grows on coastal plain as well as at higher elevations in the mountains." Peters's specimen is unusual in having relatively few glands in the inflorescence, but it has the long, eglandular trichomes characteristic of this variety.

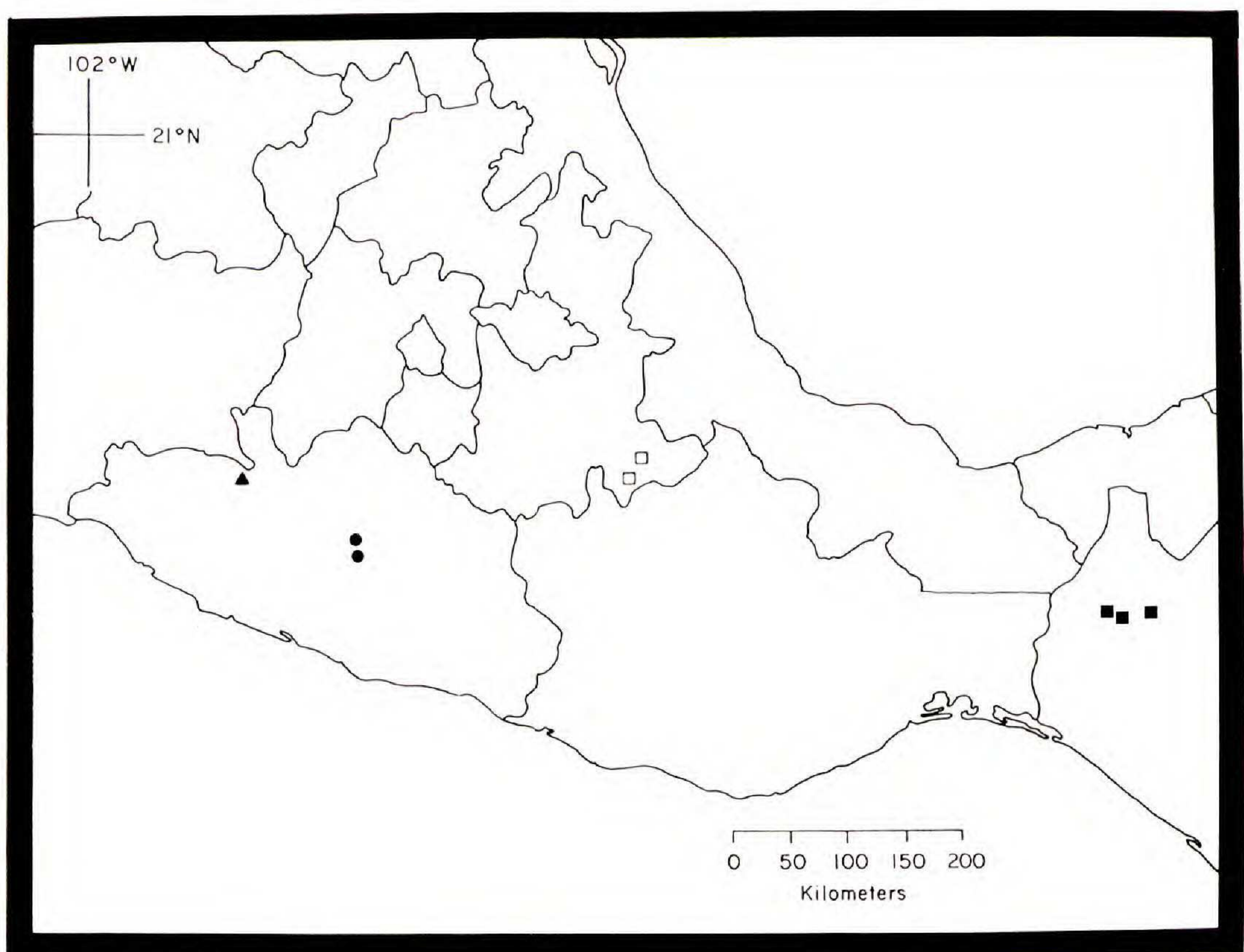
All three collections of this variety from the Cape Region are unusual in their pubescence. The trichomes of the younger stems are scaberulous and 0.05–0.2 mm long, resembling those of *Holographis virgata* subsp. *glandulifera* var. *glandulifera*. The surfaces of the leaves are also scaberulous, but the margin and the veins have the long, flexuose trichomes characteristic of *H. virgata* subsp. *glandulifera* var. *palmeri*.

Although some duplicates of *A. Carter & Ferris* 3819 from the Sierra de la Giganta contain both *Holographis virgata* subsp. *glandulifera* var. *glandulifera* and *H. virgata* subsp. *glandulifera* var. *palmeri*, Ms Carter notes (pers. comm.) that the material of the latter variety was collected at about 688 m. Material of the former variety (*A. Carter & Ferris* 3829a) was collected on the same day at about 584 m. It is not known if some of these collections were inadvertently mixed or if the two varieties indeed grow together. The difference in elevation between these two collections is not great.

3. *Holographis argyrea* (Leonard) T. F. Daniel, comb. nov.

Lundellia argyrea Leonard, *Wrightia* 2: 1. 1959. TYPE: Mexico, Guerrero, cliff along stream near Chilpancingo, km 276, 21 Oct. 1943, *Lundell* 12603 (holotype, US!; isotypes, LL, MICH!).

Erect, rounded shrub to 1 m tall. Older stems splitting in several lines, giving rise to numerous pronounced channels, glabrate; younger stems purplish, epi-



MAP 3. Southern Mexico, showing distribution of *Holographis argyrea* (solid dots), *H. hintonii* (solid triangle), *H. parayana* (solid squares), and *H. pueblensis* (open squares).

dermis soon becoming silvery white, quadrate to ellipsoid in cross section, the surface fluted, evenly pubescent, with trichomes often very sparse, eglandular, retrorse, 0.05 mm long or less. Leaves opposite, ascendant to horizontal; petiole to 10 mm long, pubescent like stems; lamina ovate to orbicular (to obovate), rounded to acute (to subattenuate) at base, rounded to acute at apex, 12–64 by 10–35 mm, 0.9 to 2.2 times longer than wide, the margin entire, flat to subrevolute, ciliate with erect to flexuose trichomes 0.05–0.6 mm long, especially near base, the surfaces sparsely pubescent or subglabrous (surfaces of unfolding leaves densely tomentose with dendroid trichomes), abaxial surface punctate. Inflorescences densely bracteate, terminal spikes to 4.5 cm long; axes pubescent with mixture of glandular and eglandular trichomes, the former 0.2–0.5 mm long, the latter erect, 0.1–0.3 mm long; flowers opposite at spike nodes; bracts lanceolate, 5.5–7 by 2–2.5 mm, pubescent like inflorescence axis; bractlets lance-subulate, approximately same length as subtending bract, 5–6.5 by 0.7–1.2 mm, pubescent like bracts. Calyx 6.5–7.5 mm long, the lobes lance-subulate, pubescent like bracts; corolla yellow with maroon markings, vertical at anthesis, 7–9.5 mm long, pubescent on outer surface with eglandular trichomes, the tube 5–5.5 mm long, slightly ampliate, the upper lip 1–2.5 mm long, with lobes 0.5–1.5 mm long, the lower lip 3.5–4 mm long, with lobes spatulate, 2.5–3.5 by 1.5–3.5 mm; stamens 1.5 mm long, the filaments 0.5 mm long, pubescent, the thecae 1–1.3 mm long, pubescent; staminode 0.2–0.3 mm long, glabrous; ovary glabrous, the style 4 mm long, glabrous, flared at apex,

the stigma unequally bilobed, with longer lobe to 0.5 mm long. Capsules not seen.

DISTRIBUTION AND HABITAT. Known only from semiarid Río Balsas basin in central Guerrero (MAP 3); rocky cliffs in low, deciduous thorn forest ca. 700 m alt.; with columnar cacti.

FLOWERING AND FRUITING. Collected only during late October, but undoubtedly flowering well into November; fruiting apparently several weeks after flowering.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** GUERRERO: Cañón de Zopilote, along road to Filo de Caballo, 0.6 mi W of jct. Hwy. 95, *T. Daniel 1193* (ASU, ENCB, GH, MICH), 1242 (CAS, DUKE, MEXU, MICH).

Leonard (1959, p. 1) noted a relationship of *Holographis argyrea* with *Aphelandra*. He believed the genus *Lundellia* could be distinguished from *Aphelandra* by its corky, fissured stems, its oval, silvery laminas, its dendroid hairs, and its "compact solitary terminal glandular spikes of small yellow flowers with their deeply included, almost sessile stamens. . . ." Although *H. argyrea* would be an anomaly in *Aphelandra*, none of these features distinguish it from *Holographis*. Its closest relative appears to be *H. virgata*; both have opposite leaves, silvery stems, and terminal spikes.

4. ***Holographis ilicifolia*** Brandege, *Zoe* 5: 236. 1906. TYPE: Mexico, Coahuila, Peña (25°28'N, 102°34'W), Feb. 1905, *Purpus 1327* (holotype, UC!; isotypes, GH!, MO!, NY!). FIGURE 3.

Twiggy, erect to spreading, often rounded subshrub to 3(–5) dm tall, arising from stout or tortuous woody base to 10 mm in diameter. Older stems woody, pubescent or glabrate; younger stems green, terete in cross section, the surface smooth to striate, evenly and densely pubescent, often making the stems appear pallid, the trichomes eglandular, retrorse to erect, 0.05–0.2 mm long. Leaves whorled, ascendant or decurved, sessile to subsessile; petiole (if present) 0.1–0.5 mm long, pubescent; lamina coriaceous, orbicular, usually partially folded lengthwise along midvein, cuneate to truncate to subcordate at base, acute-aristate at apex with spine to 3 mm long, (1.5–)3–10 by 2.8–10 mm, 0.8 to 1.3 times longer than wide, the margin spinose toothed, with spines remote, 3 to 6 per side, 0.1–1.5 mm long, the surfaces sparsely pubescent, with trichomes erect to retrorse, 0.01–0.2 mm long. Inflorescences axillary spikes to 4 cm long; axes pubescent like younger stems; flowers alternate along spike axis; bracts ovate to triangular to subulate, (1–)1.5–3 by 0.6–1 mm, pubescent like inflorescence axis; bractlets subulate, longer than subtending bract, (2–)2.5–4 by 0.6–1 mm. Calyx 5–8 mm long, lobes linear-subulate, outer surface pubescent like inflorescence axis, margin densely ciliate with flexuose, eglandular trichomes to 0.3 mm long and glandular trichomes to 0.05 mm long; corolla yellow, usually with dull maroon markings on outer surface, 10–14 mm long, pubescent on outer surface with eglandular trichomes, the tube 5–7 mm long, ampliate above, the upper lip 4–5.5 mm long, with lobes 1–3 mm long; the lower lip 5–7.5 mm long, with lobes spatulate, 4–5.5 by 2.5–4 mm; stamens 4.5–6 mm long, the filaments 3.5–4.5 mm long, more or less densely pubescent

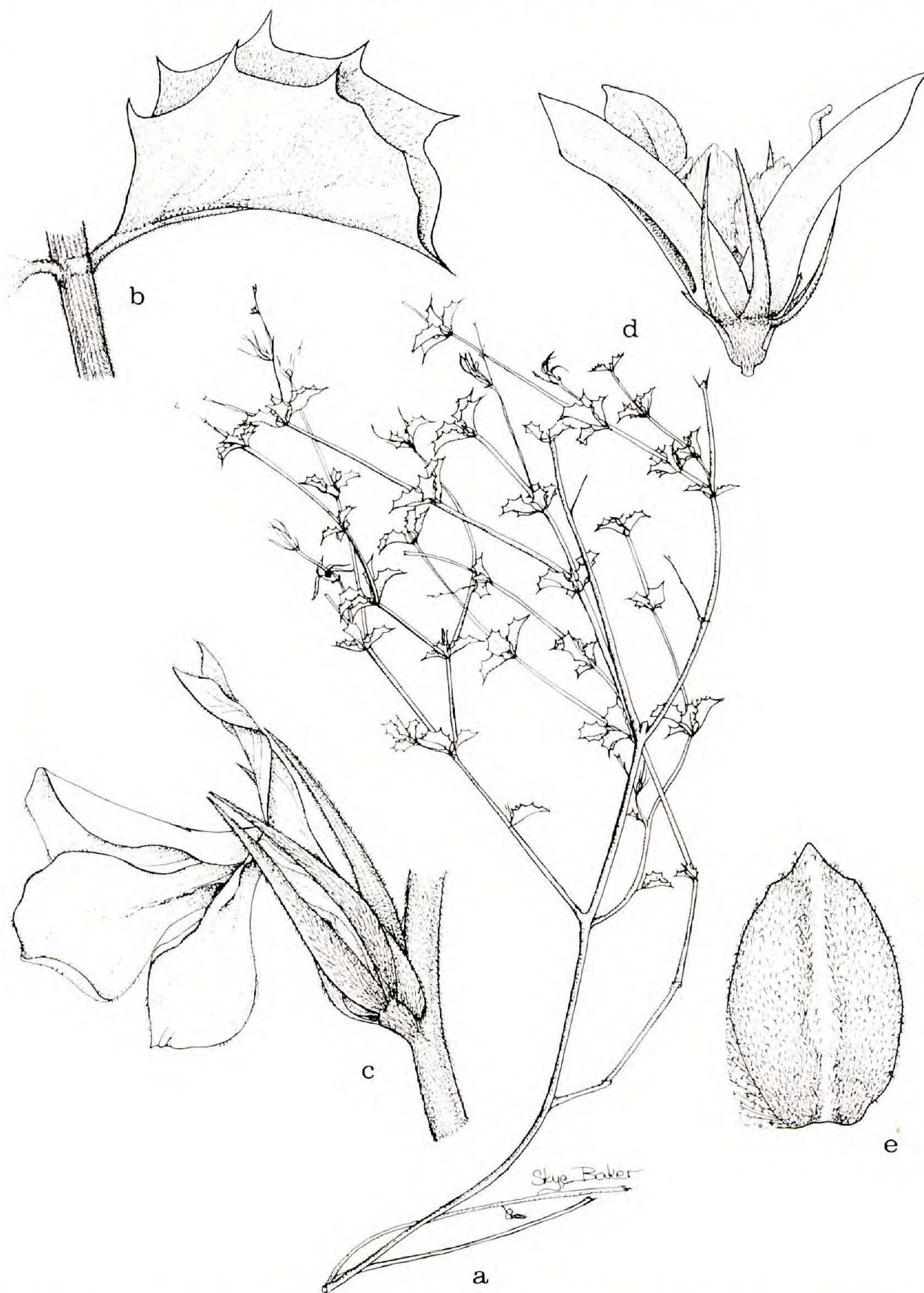


FIGURE 3. *Holographis ilicifolia*: a, habit (T. Daniel 659), $\times 0.6$; b, leaf (T. Daniel 674), $\times 7$; c, flower (T. Daniel 674), $\times 3.5$; d, capsule (Correll & I. Johnston 21435), $\times 3.8$; e, seed (Correll & I. Johnston 21435), $\times 10.5$.

with trichomes to 0.3 mm long, the thecae 1.2–1.5 mm long, pubescent along dorsal side; staminode 0.5–0.9 mm long, pubescent at base if at all; style 6–8.5 mm long, glabrous, flared at apex, the stigma lobes indistinct. Capsules brown, ellipsoid, 8–10 mm long, 2–3.5 mm in diameter, glabrous or pubescent,

trichomes to 0.1 mm long (rarely restricted to apex); retinacula 1–1.5 mm long. Seeds oval, asymmetric at base, 2.5–3.5 by 1.5–3 mm, densely pubescent with dendroid trichomes to 0.5 mm long.

DISTRIBUTION AND HABITAT. Central and southwestern Coahuila and adjacent regions of northern Durango (MAP 1); on rocky slopes and ridges and in gravelly washes of desert scrub zone, 850–1600 m alt.; with species of *Larrea* Cav., *Agave*, *Viguiera*, *Yucca* L., *Fouquieria*, *Acacia*, *Hechtia*, *Mortonia* A. Gray, *Colubrina*, *Randia* L., *Parthenium* L., *Dasyilirion* Zucc., *Leucophyllum* Humb. & Bonpl., *Jatropha*, *Mimosa*, and *Opuntia*.

FLOWERING AND FRUITING. Flowering February through September; fruiting during same period.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** COAHUILA: Puerto de Ventanillas along Hwy. 30 N of San Pedro, 7.1 mi SW of turnoff to Delicias, *T. Daniel* 659 (ASU, GH, MEXU, MICH, TEX, US); Valle de San Lucas in Sierra del Venado, N of El Mezquite, 7.5 mi W of Hwy. 30, *T. Daniel* 674 (DUKE, ENCB, MICH); ca. 23 mi NW of Las Delicias in valley N of Sierra de las Delicias, *Henrickson* 6110 (ASU); ca. 32 mi NE of Tlahualilo in NW portion of Sierra de las Delicias, *Henrickson* 12217 (MICH); ca. 72 mi SW of Cuatro Ciénegas on E side of Sierra de las Delicias, 1.5 mi SW of Las Delicias, *Henrickson* 12257 (MICH); ca. 67 mi SW of Cuatro Ciénegas, 1.5 mi SW of Las Delicias, *Henrickson* 12466 (ASU); vic. of Aguaje del Pajarito, 2–3 km N of Puerto Colorado, *I. Johnston* 8675 (F, GH, LL); NE edge of Cerro Bolas, 10.7 km SW of El Solon on Rte. 40, *M. Johnston et al.* 8282 (LL); 12.6 km NNE of Las Margaritas in canyon in E face of Sierra de las Margaritas, *M. Johnston et al.* 9504b (LL), 9517 (LL), 10362A (LL); Cañón de Fora, ca. 35 km W of Cuatro Ciénegas, *M. Johnston* 10910 (LL); S part of Sierra de los Organos, 9.5 km E of Puerto del Gallo, *M. Johnston et al.* 12137 (LL); ca. 7 mi W of Cuatro Ciénegas, *M. Powell et al.* 2286 (TEX, WIS); Cañón de la Fora, ca. 1.1 mi by road E of Est. Socorro, *Wendt & Lott* 1199 (LL); 22 mi W of Cuatro Ciénegas, *White* 1949 (ARIZ, GH, MEXU, MICH). DURANGO: 7 mi SE of Conejos, *Correll & I. Johnston* 21435 (LL, US).

Brandeggee (1906) was somewhat doubtful of the generic position of this species when he described it based on Purpus's collection from southwestern Coahuila. He stated (p. 237), "This plant is not strictly congeneric with the little known genus *Holographis*, but it seems best to place it there." Standley did not see any specimens of *H. ilicifolia* and did not include a description of it in his treatment of the Acanthaceae of Mexico (1926).

Now known rather extensively from the Chihuahuan Desert region, this species is the most unusual in the genus. It is unique among the known species of *Holographis* in its spinose-toothed, conduplicate leaves and its alternate arrangement of flowers along the spikes. In addition, the orientation of the corolla is somewhat intermediate between vertical and horizontal, and the staminode arises from the corolla up to 2 mm beyond the filaments of the fertile stamens. Although the generic position of this apparently highly specialized species is no longer in doubt, its closest relatives are not obvious.

5. ***Holographis parayana*** Miranda, *Anales Inst. Biol. Univ. Nac. México* **24**: 94. 1953. TYPE: Mexico, Chiapas, arriba La Chacona, cerca de la carretera a San Fernando, unos 10 km NO de Tuxtla Gutiérrez, 7 Jan. 1951, *Miranda* 6812 (holotype, MEXU!; isotype, F!).

Erect shrub to 2.5 m tall. Older stems pubescent or glabrate; younger stems greenish to purplish, terete to subquadrate in cross section, the surface striate, evenly pubescent, with trichomes ascendant-appressed, 0.1–0.3 mm long. Leaves whorled, ascendant to horizontal; petiole to 4 mm long, pubescent; lamina lance-ovate to ovate, attenuate to acute to truncate at base, acute at apex, 7–50 by 3.5–15 mm, 1.5 to 3.3 times longer than wide, the margin entire, flat, ciliate, the surfaces pubescent, abaxial surface often more densely so. Inflorescences axillary spikes to 1 cm long; axes pubescent with eglandular, ascendant to flexuose trichomes 0.05–0.3 mm long, occasionally also with glandular trichomes to 0.1 mm long; flowers opposite at spike nodes; bracts triangular to lance-subulate, 2–2.8 by 0.9–1.2 mm, pubescent like inflorescence axis; bractlets triangular to lance-subulate, shorter than subtending bract, 1.5–2 by 0.8–1 mm, pubescent like bracts. Calyx 2–3 mm long, the lobes lance-subulate, pubescent like bracts; corolla pinkish (label data), horizontal at anthesis, 9–10 mm long, pubescent on outer surface with mixture of glandular and eglandular trichomes, the tube 3.5–4 mm long, ampliate above, the upper lip 3–3.5 mm long, with lobes 1–1.5 mm long, the lower lip 4.8–6 mm long, with lobes spatulate, 3–3.5 by 1–2 mm; stamens 3 mm long, the filaments 2 mm long, sparsely pubescent, anterior pair often more densely so, the thecae 1.2–1.5 mm long, very sparsely pubescent; staminode 1 mm long, pubescent at apex; ovary glabrous, the style 5–6 mm long, glabrous, not conspicuously flared at apex, the stigma unequally bilobed, longer lobe to 0.5 mm long. Capsules 12–13.5 mm long, 5 mm in diameter, glabrous; retinacula 3 mm long. Seeds nearly circular in outline, 2.5 mm in diameter, pubescent with dendroid trichomes 0.1–0.3 mm long.

DISTRIBUTION AND HABITAT. Known only from vicinity of Tuxtla Gutiérrez, west-central Chiapas (MAP 3); low deciduous forests at ca. 900 m alt.

FLOWERING AND FRUITING. Flowering in January; fruiting in June.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: cerca y arriba Piñitas, NE Tuxtla G., *Enriquez 6851* (MEXU); arriba Encañada, NO Tuxtla G., *Miranda 5874* (MEXU); arriba Chacona–San Fernando, NO Tuxtla G., *Miranda 6827* (US); Chacona, *Miranda 7209* (MEXU).

Miranda (1953) noted the relationship between this species and *Holographis ehrenbergiana*. He claimed that the two could be distinguished by the flat and larger leaves, the smaller flowers, and the strongly curved corolla tube of *H. parayana*. Comparison of numerous characters in all of the species of *Holographis* indicates that the affinities of *H. parayana* are probably with *H. hintonii* and *H. anisophylla*, with which it shares numerous features including a relatively short, glandular corolla.

6. *Holographis anisophylla* T. F. Daniel, sp. nov.

FIGURE 4.

Frutex erectus. Caules juniores pubescentes trichomatibus eglandulosis 0.05–0.1 mm longis. Folia verticillata, in quoque nodo quatuor; laminae lanceolatae vel lanci-ovatae, 9–27 mm longae, 2–8 mm latae, 2.2–4.5-plo longiores quam latiores, marginibus planis ciliatis. Inflorescentia spicata; bracteae lanci-ovatae

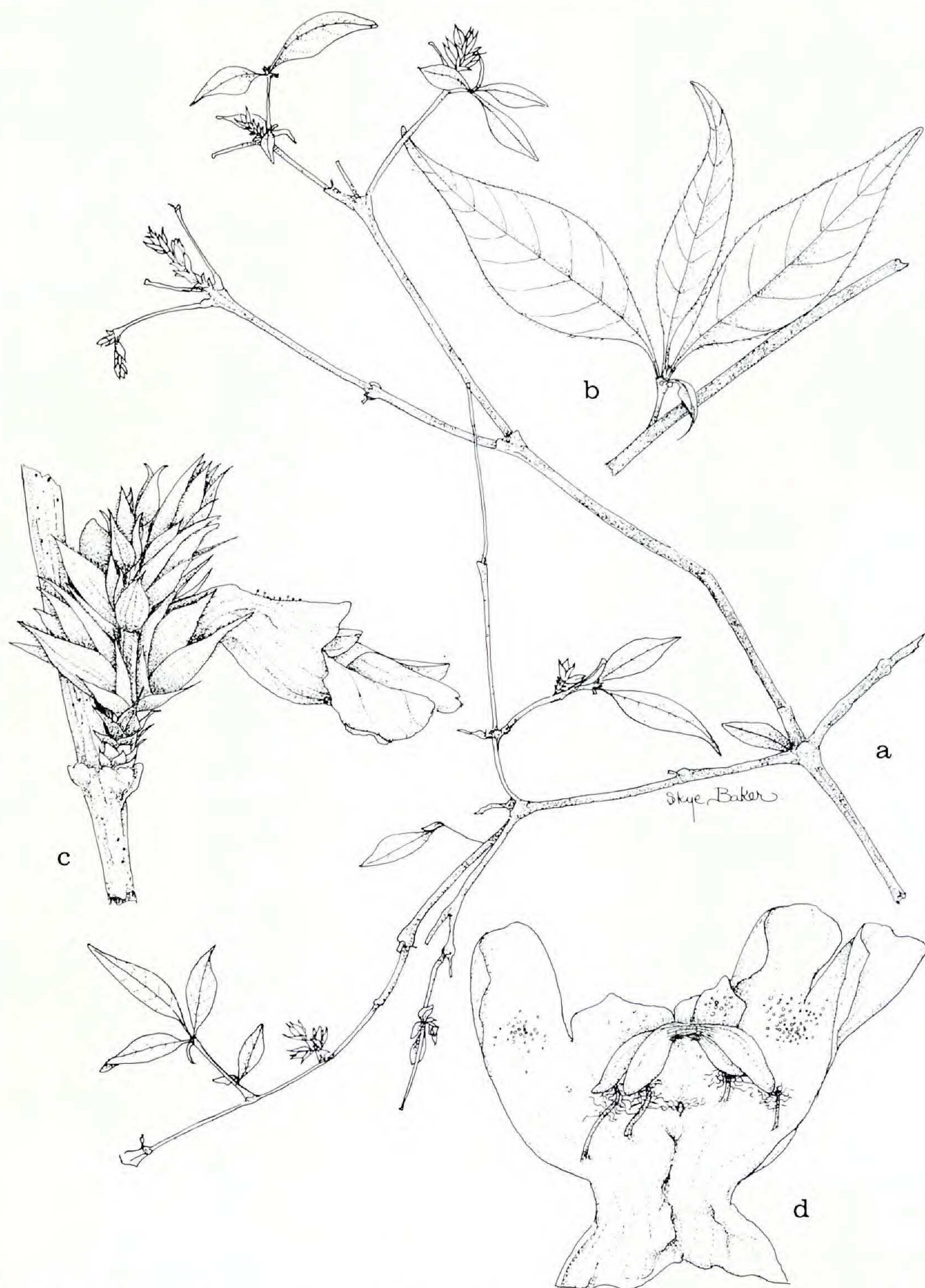


FIGURE 4. *Holographis anisophylla* (from holotype): a, habit, $\times 0.7$; b, node with leaves, $\times 1.4$; c, spike with mature flower, $\times 3.8$; d, dissected flower, $\times 5$.

vel ovatae, 2.5–3 mm longae, 1–2 mm latae; bracteolae lanci-ovatae vel ovatae, 2–2.8 mm longae; calyx 4.5–5 mm longus; corolla 8–9 mm longa, utrinque glandulosa; stamina 2.5–3 mm longa filamentis 1.3–1.6 mm longis; staminodium 0.3 mm longum, apice pubescens; stylus 3.5 mm longus glaber, ovarium basi glabrum, apice pubescens. Capsula ignota.

Erect shrub. Older stems glabrate; younger stems purplish turning white, terete in cross section, the surface striate, pubescent with eglandular, retrorse trichomes 0.05–0.1 mm long, trichomes more or less evenly distributed or in 2 vertical lines. Leaves whorled, horizontal to ascendant, sessile to subsessile; petiole, if present, to 1 mm long; lamina lanceolate to lance-ovate, long-attenuate at base, acute to acuminate (to falcate) at apex, 9–27 by 2–8 mm, 2.2 to 4.5 times longer than wide, the 4 leaves at each node unequal in size, with leaves subtending inflorescences considerably reduced, the margin entire, flat, ciliate with ascendant trichomes to 0.5 mm long, the surfaces pubescent. Inflorescences axillary spikes to 17 mm long; axes pubescent with mixture of glandular and eglandular trichomes, the former 0.05 mm long, the latter erect, 0.05–0.1 mm long; flowers opposite at spike nodes; lower bracts (up to 7 series) sterile, triangular, 1–2 mm long; upper bracts fertile, lance-ovate to ovate, 2.5–3 by 1–2 mm, mucronate at apex, pubescent like inflorescence axis, margin lanate with trichomes to 0.5 mm long; bractlets lance-ovate to ovate, approximately same length as subtending bract or slightly shorter, 2–2.8 by 1 mm, mucronate at apex. Calyx 4.5–5 mm long, the lobes lanceolate, mucronate at apex, pubescent like bracts; corolla horizontal at anthesis, color unknown, 8–9 mm long, pubescent on outer surface with mixture of glandular and eglandular trichomes, the tube 4–5 mm long, ampliate above, the upper lip 1.5–2 mm long, with lobes 1 mm long, the lower lip 4 mm long, with lobes obovate, 2.5 by 2.5–2.8 mm; stamens 2.5–3 mm long, the filaments 1.3–1.6 mm long, pubescent with flexuose trichomes to 0.8 mm long, the thecae 1.8–2 mm long, connivent at pubescent apex; staminode 0.3 mm long, pubescent at apex; ovary glabrous below, pubescent with eglandular trichomes at apex, the style 3.5 mm long, glabrous, the stigma lobes equal, 0.4 mm long. Capsules not seen.

TYPE. Mexico, Colima, Desviación cerca Río Salado, 4 Dec. 1959, *Miranda 9052* (holotype, MEXU!).

Holographis anisophylla is known only from the type, a flowering collection from east-central Colima (MAP 1), which was collected in tropical deciduous forest (McVaugh, pers. comm.). It is unique among the known species of *Holographis* in having glands on the inner, as well as the outer, surface of the corolla. It appears to be most closely related to *H. pallida*, a species that occurs approximately 800 km to the northwest of the type locality. Miranda's collection was, in fact, originally identified as the latter species. These two species resemble each other in the form of the cauline trichomes and in the shape of the leaves and bracts; in addition, the whorled leaves of *H. pallida* are frequently anisophyllous. The species can be distinguished from each other by the characters in the following couplet:

1. Bracts 3–5 mm long; bractlets lance-subulate, 3–4 mm long; calyx 5–7 mm long; corolla 10–12 mm long, eglandular; stamens 3.5–4 mm long. *H. pallida*.
1. Bracts 2.5–3 mm long; bractlets lance-ovate to ovate, 2–2.8 mm long; calyx 4.5–5 mm long; corolla 8–9 mm long, glandular; stamens 2.5–3 mm long.
 *H. anisophylla*.

7. *Holographis hintonii* (Leonard) T. F. Daniel, comb. nov.

Berginia hintonii Leonard, Kew Bull. **1938**: 64. 1938. TYPE: Mexico, Guerrero, District of Coyuca, between Coyuca de Catlán and Chamerito, 26 April 1934, *Hinton et al.* 5956 (holotype, K!).

Erect shrub. Older stems covered with conspicuous lenticels, glabrous; younger stems subquadrate in cross section, the surface striate-fluted, sparsely pubescent in 2 vertical lines, with trichomes inconspicuous, eglandular, retrorse, 0.05–0.1 mm long. Leaves whorled; petiole up to 8 mm (or more?) long, pubescent with erect to flexuose trichomes to 0.2 mm long; lamina apparently ovate-elliptic (see discussion), attenuate at base, to about 45 (or more?) by 20 (or more?) mm, the margin entire, flat, ciliate, the surfaces sparsely pubescent with flexuose trichomes to 0.8 mm long, the veins on the lower surface densely pubescent. Inflorescences congested axillary spikes to 10 mm (or more?) long; axes obscured by dense mats of crooked, interwoven trichomes to 0.8 mm long (villous); flowers opposite at spike nodes; lower bracts (up to 4 series) sterile, triangular, smaller than upper bracts; upper bracts fertile, broadly ovate to orbicular, 1.5–2 by 1.2–1.5 mm, mucronate at apex, pubescent with mixture of erect glandular and eglandular trichomes to 0.2 mm long, margin villous-ciliate; bractlets lanceolate, approximately same length as subtending bract, 1.5–2 by 0.7–0.9 mm, mucronate at apex, pubescent like bracts. Calyx 4–4.5 mm long, the lobes lanceolate, pubescent like bracts (but glands often more numerous and conspicuous); corolla color unknown, orientation unknown, 8–9.5 mm long, pubescent on outer surface with mixture of eglandular and glandular trichomes, the tube 2–2.5 mm long, the upper lip 3–4 mm long, with lobes 2–3 mm long, the lower lip 6–7 mm long, with lobes orbicular, 3–3.5 mm in diameter; stamens 3–3.5 mm long, the filaments 1–1.5 mm long, densely pubescent with flexuose trichomes to 0.8 mm long, the thecae 2 mm long, sparsely pubescent; staminode 0.4 mm long, glabrous; style 4 mm long, pubescent, the stigma lobes 0.5 mm long. Capsules 10–11 mm long, 3–4 mm in diameter, pubescent, with trichomes eglandular, 0.1–0.2 mm long. Seeds 4 by 2.5 mm, pubescent with dendroid trichomes to 0.3 mm long.

This species is presently known only from the type, which was collected in flower and fruit in late April in the semiarid region of northwestern Guerrero (MAP 3). Although this specimen of *Holographis hintonii* is leafless, the size of the leaf scars and a fragment of the basal portion of a leaf in a packet attached to the specimen indicate relatively large, petiolate, ovate-elliptic leaves, probably similar in form to those found in *H. tamaulipica*.

When he described this species (as *Berginia hintonii*), Leonard (1938) noted that it was distinctive in *Berginia* in having “short bract-covered peduncles and short tomentose spikes.” In *Holographis* its closest relatives appear to be *H. parayana* and *H. anisophylla*; all three have entire, flat leaves and relatively small (8–10 mm long), glandular corollas.

8. **Holographis pallida** Leonard & Gentry in Gentry, *Brittonia* 6: 324. *fig.* 5. 1948. TYPE: Mexico, Sinaloa, Cerro Llano Redondo, W of Caymanero, 25 April 1944, *H. Gentry* 7022 (holotype, MICH!; isotypes, DES!, F!, GH!, NY!, US!).

Erect shrub to 1.3 m tall. Older stems pubescent or glabrate; younger stems gray-green, terete in cross section, the surface smooth to striate, evenly and densely pubescent making the stems appear pallid, the trichomes eglandular, retrorse, 0.05–0.2 mm long. Leaves whorled, ascendant or decurved, subsessile to petiolate; petiole to 5 mm long, pubescent like younger stems; lamina lanceolate to ovate to subelliptic, long-attenuate at base, acute to acuminate (to falcate) at apex, 8–50 by (2–)4–21 mm, 2.5 to 4 times longer than wide, the 4 leaves at a node often unequal in size, the margin entire, flat, ciliate, the surfaces sparsely pubescent, with trichomes often restricted to major veins, abaxial surface somewhat punctate. Inflorescences densely bracted axillary spikes to 3 cm long; axes hirsute, with trichomes erect to recurved, 0.2–0.8 mm long (axes often with inconspicuous, capitate glands to 0.3 mm long as well); flowers opposite at spike nodes; lower bracts (up to 4 series) mostly sterile, triangular, 1–2 mm long; upper bracts fertile, lanceolate to ovate, 3–5 by 1–1.8 mm, mucronate at apex, pubescent like inflorescence axis, with trichomes particularly evident along margin; bractlets lance-subulate, approximately same length as subtending bract, 3–4 by 0.8–1 mm, mucronate at apex. Calyx 5–7 mm long, the lobes lance-subulate, mucronate at apex, pubescent like bracts; corolla “white to pale lavender” (label data), horizontal at anthesis, 10–12 mm long, pubescent on outer surface with eglandular trichomes, the tube 5–6 mm long, ampliate above, the upper lip 2–3 mm long, with lobes 0.8–1.5 mm long, the lower lip 5–6 mm long, with lobes spatulate, 3–5 by 2–4 mm; stamens 3.5–4 mm long, the filaments 1.5–2 mm long, pubescent with flexuose trichomes to 0.4 mm long, the thecae 1.5–2 mm long, pubescent along dorsal side, connivent around style; staminode reduced to minute, glabrous projection 0.1 mm long; style 5.3–6 mm long, glabrous or sparsely pubescent, flared at apex, the stigma equally bilobed, with lobes to 0.5 mm long. Capsules 7–9 mm long, 3 mm in diameter, pubescent on outer surface with eglandular trichomes 0.1–0.2 mm long; retinacula 1.5 mm long. Seeds oval, 2.2 by 1.9 mm, densely pubescent with dendroid trichomes to 0.2 mm long.

DISTRIBUTION AND HABITAT. Southern Sonora and central Sinaloa (MAP 1); in arroyos and on rocky slopes in thorn forest, ca. 50–500 m alt.

FLOWERING AND FRUITING. Flowering in February and April, when leaves appear to begin flushing; fruiting in April.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** SONORA: San Bernardo, *H. Gentry* 1350 (A, ARIZ, DES, F, MO, UC), 3615 (ARIZ, F); Sierra Bojihuacame, SE of Cd. Obregón, *H. Gentry* 14492 (US).

Leonard and Gentry (*in* Gentry, 1948) noted the apparent uniqueness among American Acanthaceae of the monothealous stamens with connivent anthers in this species and suggested that the plant may be worthy of generic status.

In the present study this character was found to be almost universal among species of *Holographis*. Leonard and Gentry further noted the similarity of this species to members of *Berginia*; indeed, Gentry's label on the type bears a preliminary name in this genus. Finally, they concluded that *Holographis* and *Berginia* were probably congeneric.

The closest relative of *Holographis pallida* appears to be *H. anisophylla*. The similarities between them are discussed under the latter species.

9. ***Holographis pueblensis*** T. F. Daniel, sp. nov.

FIGURE 5.

Suffrutex vel frutex erectus usque ad 5 dm altus. Caules juniores pubescentes trichomatibus eglandulosis, 0.2–0.8 mm longis. Folia supera verticillata, in quoque nodo quatuor; laminae ovatae vel ellipticae, 5–24 mm longae, 3–15 mm latae, 1.5–2-plo longiores quam latiores, marginibus revolutis ciliatis. Inflorescentia spicata; bracteae anguste lanceolatae vel lanci-subulatae, 6.5–11 mm longae, 1.5–2 mm latae; bracteolae lanci-subulatae, 5.5–9 mm longae. Calyx 7–10.5 mm longus; corolla aurea, 15–18 mm longa, extus pubescens; stamina 9–11 mm longa filamentis 8–8.5 mm longis apicibus glabris basibus pubescentibus; staminodium 0.4–0.5 mm longum pubescens; stylus 12–16 mm longus glaber, ovarium glabrum.

Erect subshrub to shrub to 5 dm tall arising from stout, woody base to 5 mm in diameter. Older stems pubescent or glabrate; younger stems terete in cross section, the surface smooth to striate, evenly (often densely) pubescent, with trichomes eglandular, ascendant-appressed, 0.2–0.8 mm long. Leaves whorled (lower leaves sometimes opposite or subopposite), ascendant to horizontal, subsessile to petiolate; petiole to 8 mm long, pubescent with flexuose to ascendant trichomes to 1 mm long; lamina ovate to elliptic, attenuate to acute to truncate at base, acute to rounded at apex, 5–24 by 3–15 mm, 1.5 to 2 times longer than wide, the margin entire, revolute, ciliate, the surfaces pubescent, the abaxial surface often punctate. Inflorescences axillary, densely bracted spikes to 4.5 cm long; axes pubescent with erect to ascendant trichomes 0.2–0.5 mm long; flowers opposite at spike nodes; bracts narrowly lanceolate to lance-subulate, 6.5–11 by 1.5–2 mm, tapering to point but not mucronate at apex, pubescent like inflorescence axis; bractlets lance-subulate, approximately same length as subtending bract, 5.5–9 by 1–1.8 mm, pubescent like bracts. Calyx 7–10.5 mm long, the lobes lance-subulate, outer surface sparsely pubescent (often glabrous near base), margin lanate; corolla yellow, vertical at anthesis, 15–18 mm long, pubescent on outer surface with eglandular trichomes, the tube 7.5–9 mm long, ampliate above, the upper lip 7–8 mm long, with lobes 0.3–0.5 mm long, the lower lip 7.5–9 mm long, with lobes spatulate, 4.5–6.5 by 2.2–4 mm; stamens 9–11 mm long, the filaments 8–8.5 mm long, glabrous above, pubescent at base, the thecae 2–3 mm long, pubescent; staminode 0.4–0.5 mm long, pubescent; ovary glabrous, the style 12–16 mm long, glabrous, not flared at apex, the stigma lobes inconspicuous. Capsules not seen.

TYPE. Mexico, Puebla, vicinity of San Luis Tultitlanapa, near Oaxaca, July 1908, *Purpus* 3346 (holotype, UC!; isotypes, F!, GH!, MO!, NY!, US!).



FIGURE 5. *Holographis pueblensis*: a, habit (*Purpus s.n.*, June 1907), $\times 0.6$; b, node with leaves (*Purpus* 3346), $\times 2.5$; c, young spike with flowers (*Purpus* 3346), $\times 2.2$; d, gynoecium (*Purpus* 3346), $\times 3$.

DISTRIBUTION AND HABITAT. Known only from two Purpus collections from semiarid regions of southeastern Puebla (MAP 3).

FLOWERING AND FRUITING. Flowering June and July; time of fruiting unknown.

ADDITIONAL SPECIMEN EXAMINED. **Mexico.** PUEBLA: Tehuacán, *Purpus s.n.*, June 1907 (UC).

This species appears to be most closely related to *Holographis ehrenbergiana*, which occurs primarily north of the range of *H. pueblensis* (see discussion under *H. ehrenbergiana*).

10. **Holographis ehrenbergiana** Nees in DC. Prodr. **11**: 728. 1847. TYPE: Mexico, "supra la Hacienda de Guadela [?]," *Ehrenberg 1224* (holotype, B, destroyed). FIGURE 6.

Erect, often rounded subshrub to shrub to 1.3 m tall, arising from stout, often tortuous woody base to 12 mm in diameter. Older stems pubescent or glabrate; younger stems pale green, terete to subquadrate in cross section, the surface smooth to striate, evenly (often densely) pubescent, with trichomes eglandular, erect to ascendant, 0.1–0.7 mm long. Leaves whorled, ascendant to horizontal, subsessile to petiolate; petiole to 8 mm long, pubescent; lamina lanceolate to obovate, attenuate to acute at base, acute to rounded at apex, 5–35 by 2–16 mm, 1.9 to 3.5 times longer than wide, the margin entire, revolute, ciliate, the surfaces pubescent, abaxial surface often more densely so (sometimes becoming lanate). Inflorescences axillary spikes to 2 cm long, usually reduced to 2 flowers; axes pubescent like younger stems; bracts triangular to subulate, 1.5–5 by 0.5–1 mm, emucronate, sparsely to densely pubescent with erect to flexuose trichomes to 1 mm long; bractlets subulate, approximately same length as subtending bract or slightly longer, (1.5–)2.5–5 by 0.5 mm, pubescent like bracts. Calyx 3.5–6 mm long, the lobes lance-subulate, pubescent like bracts; corolla yellow, vertical at anthesis, 12–18 mm long, pubescent on outer surface with eglandular trichomes, the tube 6–10 mm long, ampliate above, the upper lip (6–)7.5–9 mm long, with lobes 0.3–1 mm long, the lower lip (5.5–)8–10 mm long, with lobes spatulate, 4.5–6 by 2–4.5 mm; stamens 9–11 mm long, the filaments 8–10 mm long, glabrous or pubescent at base, the thecae 1.5–2.3 mm long, densely pubescent; staminode 0.5–1.3 mm long, pubescent at base; style 12–14 mm long, sparsely pubescent (some individual styles glabrous, but at least some styles sparsely pubescent on each plant), not flared at apex, the stigma lobes inconspicuous. Capsules 10–15 mm long, 4–4.5 mm in diameter, glabrous; retinacula 2–3 mm long. Seeds suboval, 3.5–4.8 by 2.5–3.5 mm, glabrous.

DISTRIBUTION AND HABITAT. Central Nuevo León and Tamaulipas south through San Luis Potosí and Hidalgo, apparently to southeastern Puebla (MAP 1); rocky limestone slopes at 150–2000 m alt.; in arid and semiarid associations with species of *Mimosa*, *Flourensia* DC., *Acacia*, *Colubrina*, *Agave*, *Neopringlea* S. Watson, *Cordia* L., *Bonetiella* Rzedowski, *Fouquieria*, and *Yucca*.

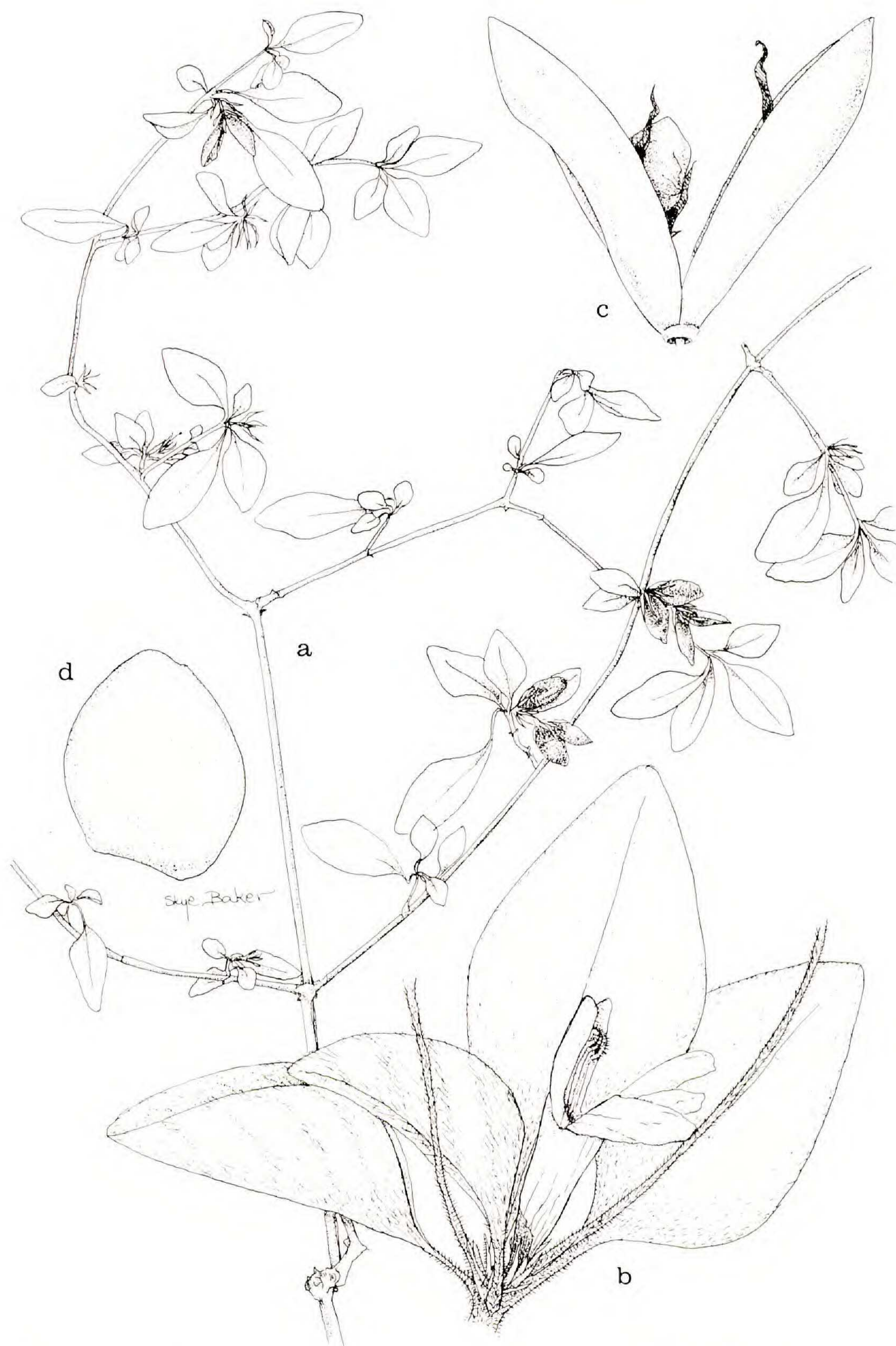


FIGURE 6. *Holographis ehrenbergiana*: a, habit (*Purpus* 4921), $\times 0.6$; b, node with leaves and flower (*Moore & Wood* 4406), $\times 2$; c, capsule (*Purpus* 4921a), $\times 3.8$; d, seed (*Purpus* 4921a), $\times 6.8$.

FLOWERING AND FRUITING. Flowering May through October; fruiting a month or two after flowering.

REPRESENTATIVE SPECIMENS. **Mexico.** HIDALGO: km 147, SE of Ixmiquilpan, *Lundell & Lundell 12342* (LL, MICH); Barranca de Tolimán, above mines on road from Zimapán to Mina Loma del Toro and Balcones, *Moore & Wood 4406* (A, MEXU, MICH, UC, US); Ixmiquilpan, *Purpus 1409* (F, GH, MO, NY, UC); 10 km NW de Zimapán, *González Quintero 3238* (ENCB, MICH); 5 km NW de Actopan, *González Quintero 3581* (DS, ENCB, MICH, MSC). NUEVO LEÓN: Cañón de Huasteca, near Monterrey, near upper spring of Rancho de Ed. Aguirre-Pequeño, *Kruckeberg 4857* (MICH). PUEBLA: Tlacuilotepec, *Purpus 3936* (UC). SAN LUIS POTOSÍ: 20 km E of San Francisco on San Luis Potosí–Río Verde Hwy., 22°00'N, 100°37'W, *M. Johnston et al. 8182* (LL); 10 mi W of Río Verde on road to S.L.P. at microondas station, *M. Johnston et al. 11189* (LL); Río Verde, *Palmer 4* (F, GH, MO, NY, UC, US); Minas de San Rafael, *Purpus 4921* (F, MO, UC, US), *4921A* (GH, MO, UC), *5225* (DES, F, GH, MEXU, MO, NY, UC); E de Núñez, km 48 carretera S.L.P.–Antiguo Morelo, *Rzedowski 5605* (ENCB); ca. 15 km NE de Guadalcázar, *Rzedowski 6031* (ENCB, MEXU, MICH); 40 km S de Matehuala, 6 km E del km 575 de la carretera México–Piedras Negras, *Rzedowski 8254* (ENCB). TAMAULIPAS: Sierra de San Carlos, vic. of San Miguel, *Bartlett 10623* (F, MICH); Cerro El Platero above Rancho El Platero, 0.5 mi S of Ejido El Higuerón (Mpio. Aldama) in Sierra de Tamaulipas, *T. Daniel 268* (MICH); 1 km S of Carabanchel, *Gilbert 74* (TEX); 3 mi E of the San Fernando–Santander Jiménez Hwy. on road to Loreto, *M. Johnston & Crutchfield 5593* (MICH, TEX); by Mex. 85, 10.6 mi N of San José and 16 mi N of Ejido, *Kral 27326* (MO); Buena Vista Hda., *Wootton s.n.*, 14 June 1919 (US). Locality unknown: *Coulter 1211* (GH).

Purpus's specimen from Tlacuilotepec, Puebla, was apparently collected near where *Holographis pueblensis* was growing. Sousa Sánchez (1969) noted that Tlacuilotepec is probably in the region of San Luis Tultitlanapa. It is from this latter locality that the type of *H. pueblensis* was collected. If this locality information is correct, then the range of *H. ehrenbergiana* overlaps those of both *H. tamaulipica* and *H. pueblensis*.

Holographis ehrenbergiana shows considerable variation in the amount of pubescence on the abaxial leaf surface. At one extreme (e.g., *M. Johnston & Crutchfield 5593*) the lower leaf surface is evenly but relatively sparsely pubescent, while in some specimens (e.g., *Moore & Wood 4406*) the trichomes are so dense that the surface is not visible.

Holographis ehrenbergiana appears to be most closely related to *H. pueblensis*, which it superficially resembles. Characters of the inflorescence, bracts, bractlets, and calyx readily distinguish these species, however.

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